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Phenotypic plasticity and genetic differentiation in ruderal and agricultural populations of the weed *Senecio vulgaris* L.: implications for its biological control

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Abstract

Phenotypic plasticity and genetic differentiation of the annual weed *Senecio vulgaris* L. from ruderal and agricultural habitats were investigated to evaluate the implications for its biological control with the rust fungus *Puccinia lagenophorae* Cooke using the system management approach. To assess phenotypic plasticity and genetic differentiation of ruderal and agricultural *S. vulgaris* the population dynamics of the plant and its associated rust fungus were investigated, vegetative and reproductive responses of plants, grown in the greenhouse at different nutrient and infection levels, were compared and a reciprocal seed transplant was conducted.

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 and a majority of plants in flower and seed set in spring. At the agricultural habitat, where only a few *S. vulgaris* winter due to weed control measures, population sizes in spring were smaller with significantly more vegetative plants. The limited number of suitable hosts at the agricultural habitat in spring lead to a delay of rust infection until summer, in contras to the ruderal habitat where the rust already appeared in spring. 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*. The greenhouse experiment demonstrated that plants of *S. vulgaris* from ruderal and agricultural habitats were genetically different in their response to additional nutrients, suggesting nutrient specific genetic differentiation. Plants of *S. vulgaris* with additional nutrient applications showed a stronger response to infection by *P. lagenophorae*. Genetic differentiation of *S. vulgaris* with respect to infection by *P. lagenophorae* could not be detected. Rust infection significantly decreased leaf area, vegetative biomass and reproductive output without significant differences in the response to infection between plant families, suggesting that *P. lagenophorae* is not an important selection factor in *S. vulgaris* populations at present. This result was confirmed by the transplant experiment where a higher rust incidence did neither result in an increased disease impact nor did it affect survival of *S. vulgaris*. Successful infection of different plant families with one rust line also suggests the potential of using a single rust line as a biological control agent. Infection by the rust occurred at all transplant sites and was solely determined by the environment. It seems that fungal spores for infection are widely distributed and that in the presence of suitable hosts, infection depends on favourable conditions for spore germination.

In the absence of detectable genetic variation of *S. vulgaris* plants to infection by *P. lagenophorae* and the minor importance of the rust as a selection factor in *S. vulgaris* populations at present, the potential of the system management approach for the biological control of *S. vulgaris* is supported by the results of the present thesis. Management of the pathosystem to stimulate rust epidemics can be achieved by i) wintering of *S. vulgaris* plants as inoculum sources ii) single rust lines serving as inoculum and iii) improvement of infection conditions through irrigation and fertilisation at the time of inoculum introduction.

Key words: adaptation, biological weed control, demography, genetic differentiation, habitat, nutrients, phenotypic plasticity, *Puccinia lagenophorae*, reciprocal seed transplant, selection, *Senecio vulgaris*, system management approach

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General introduction

Weed population studies

Weed populations are 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). Weed population studies, including the dynamics and evolution of weed populations, are therefore a prerequisite to any weed control strategy. They provide information about the critical stages in the life cycle of the weed and data on mortality and fecundity can be used to predict changes in population size and growth (Van Groenendael 1988). Selective pressures and their influence on weed populations, especially the development of resistance, can be identified and controlled (Barrett 1988).

Biological weed control

Weeds are the most significant of the economic and environmental pests, and they are target of much of the pesticides applied worldwide with herbicides amounting to 47% of the world agrochemical sales (Crutwell McFadyen 1998). Toxicity to non-target beneficial or endangered organisms, to wildlife and humans as well as the improper or excessive use leading to the development of resistance in the target organism while contaminating the environment lead to a re-examination of weed control strategies. Reliance on herbicides stimulated crop production in a weed-free environment. However, the increased ecological importance of biodiversity in sustainable agro-ecosystems is not compatible with the complete eradication of weeds (Müller-Schärer *et al.* 2000). Furthermore weeds may be relevant as companion plants interfering with natural enemies of the crop (Radosevich *et al.* 1997) and to prevent erosion, water run-off and nutrient leakage (Zimdahl 1993).

Biological control has become an alternative in situations were it is necessary to control single weed species (Müller-Schärer and Frantzen 1996). Biological weed control is the deliberate use of living organisms to lower the population density or competitive ability of a weed species below its economic threshold (Radosevich *et al.* 1997). Biological control offers an economic and environmentally safe approach (Crutwell McFadyen 1998) to achieve sustainable agricultural production. In biological weed control different approaches can be distinguished.

The inoculative, or classical, approach is based on introduction of exotic control organisms from the geographical area of the weed's origin (Watson 1991) released over a small area of the total weed infestation. Originally this method was thought to be suitable for weeds in extensive agriculture such as rangelands, water ways and semi-natural areas (McWhorter and Chandler 1982), but it has been shown that annual weeds of arable crops might also be suitable targets (Andres *et al.* 1976). Successful examples of the inoculative approach comprise the introduction of the moth *Cactoblastis cactorum* (Berg.) in Australia against *Opuntia* (prickly pear) spp. (Debach and Rosen 1991) and the introduction of the rust fungus *Puccinia chondrillina* Bubak & Syd. infecting *Chondrilla juncea* L. (skeleton weed) in Australia (Cullen *et al.* 1973).

The inundative, or bioherbicide, approach is based on the use of indigenous pathogens applying massive doses of inoculum to the entire weed population. According to Charudattan (1988) the term inundative control agents should be reserved for pathogens that can be mass-produced *in vitro* and applied as herbicidal preparations. Such biological agents are generally produced, handled and applied like chemical herbicides. The inundative approach is generally used for weed control in intensive agriculture. Presently there are four bioherbicides commercially available for use: Camperico (*Xanthomonas campestris* against *Poa annua* spp. *annua* (annual meadowgrass) and *Poa pratensis* (smooth-stalked meadowgrass)) in golf lawns, Collego (*Colletotrichum gloeosporioides* f. sp. *Aeschynomene* against *Aeschynomene virginica* (nothern joint vetch)) in rice and soybean, DeVine (*Pytophtora palmivora* against *Morrenia odorata* (strangler vine)) in citrus and BioChon (*Chondrostereum purpureum* against *Prunus serotina* (black cherry)) in forests. The later is not registered as a microbial herbicide but as a wood-decaying agent for use in The Netherlands only.

The augmentative approach is based on the application of relatively low amounts of native or naturalised natural enemies and relies on the innate reproduction ability of the biocontrol agent (Charudattan 1988). The conservation approach manipulates the environment (i.e. the habitat) enhancing survival and/or performance of the control organism (Barbosa 1998).

Müller-Schärer and Frantzen (1996) redefined the various approaches to biological weed control to improve distinction among them and to take modern views of agro-ecology into account. They introduced the system management approach, which is related to the augmentative and conservation approach. It focuses on native or naturalised pathogens, emphasising the cautious manipulation of a weed pathosystem excluding disruptive events such as the introduction of exotic control organisms (inoculative approach) or the mass release of inoculum (inundative approach). The approach is thus feasible for the control of weeds where the introduction of an exotic natural enemy is not possible or the natural enemy cannot be produced in large quantities. The system management approach is aimed at managing a weed pathosystem in such a way to stimulate disease epidemics on the target weed population and reducing the competition exerted by the weed on a crop (Frantzen and Müller-Schärer 1998). This can be achieved by i) introduction of a relatively small amount of inoculum in a weed population at an appropriate time ii) careful selection and manipulation of the genetic composition of the pathogen population and iii) specific management of infection conditions (Müller-Schärer and Frantzen 1996). The system management approach is thus not aimed at eradicating the weed to obtain a weed free crop but is directed at reducing weed-induced crop losses. It is intended not only for extensive agro-ecosystems, but also for the use in intensive agriculture.

Phenotypic plasticity and genetic differentiation

Plants from natural or ruderal habitats invading agriculture face new environmental challenges. Agricultural habitats differ from natural/ruderal habitats due to human activity comprising tillage, crop planting and harvesting, fertiliser inputs, weed control and other cultivation practices. The colonising species may nevertheless increase in population size or density and result in weed populations (Putwain *et al.* 1982). Adaptation to the agricultural habitat may occur in two ways: phenotypic plasticity or genetic differentiation.

Phenotypic plasticity is the ability of an individual organism to alter its physiology/morphology in response to changes in environmental conditions (Schlichting 1986). Bradshaw (1965) emphasised that plasticity of a character appears to be i) specific for that character, ii) specific in relation to particular environmental influences iii) specific in direction iv) under genetic control and v) able to be altered by selection. Adjustment to different environmental conditions by phenotypic plasticity leads to a general-purpose genotype with broad and overlapping reactions (Schmid 1992). In contrast, genetic differentiation will lead to populations comprising a diversity of genotypes each superior over a part of the range of the environment but inferior to specialists elsewhere (Bell *et al.* 1993).

Whether natural selection will lead to adaptation through phenotypic plasticity or genetic differentiation depends on the scale of environmental variation in space and time. Large-scale spatial variation (relative to dispersal distances and competitive neighbourhoods) generally leads to specialisation and genetic variation while smaller-scale spatial variation will lead to genetic differentiation only if selection is sufficiently intense (Slatkin 1973). Bell *et al.* (1993) argued that in spatially fine-grained environments dispersing offspring are likely to encounter conditions of growth, which differ from those experienced by their parents, favouring phenotypic plasticity, while in spatially coarse-grained environments dispersing offspring are likely to encounter conditions, which are similar to those experienced by their parents, favouring genetic differentiation. Temporal variation within a generation favours general-purpose genotypes, whereas longer scales of temporal variation may not (Lynch and Gabriel 1987). The relative importance of spatial and temporal variation of the environment on plant adaptation is poorly understood (Bell *et al.* 1993).

Understanding the adaptation of natural/ruderal species to agricultural habitats is relevant improving weed control (Jordan and Jannink 1997). Information on the reproductive system and genetic structure of weed populations are especially helpful in the field of biological control (Barrett 1988). Populations that regenerate primarily by selfing, apomixis, or clonal propagation often contain less genetic variation and may be more easily controlled by biological control agents (Barrett 1982). Moreover biological control agents as potential selection factors and the likelihood of evolving resistance is an important concern for the successful implementation of biological control (Barrett 1982).

Objectives

The system management approach was contrived in the framework of COST-816 “Biological control of weeds” including *Senecio vulgaris* L. as a target weed species to be controlled with the rust fungus *Puccinia lagenophorae* Cooke (Müller-Schärer and Scheepens 1997). To further develop the system management approach the aims of the present thesis were to i) investigate the population dynamics of *S. vulgaris* and *P. lagenophorae* in ruderal and agricultural habitats ii) to assess phenotypic and genetic variation of ruderal and agricultural *S. vulgaris* populations and iii) to determine whether differential responses of *S. vulgaris* from ruderal and agricultural habitats lead to local adaptation through natural selection and iv) to resolve whether *P. lagenophorae* is or may become an important selection factor in *S. vulgaris* populations.

Study organisms

Senecio vulgaris

The annual species *S. vulgaris* (Asteraceae), the common groundsel, is subdivided into two subspecies (Harris and 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* the more frequent non-radiate variety containing only hermaphrodite disc florets and var. *hibernicus* a radiate variety bearing capitula containing an outer ring of pistillate ray florets. The ray flower character is controlled by a single gene and inheritance of ray flowers is incompletely dominant (Trow 1912). In the following the term *S. vulgaris* refers to *S. vulgaris* ssp. *vulgaris* var. *vulgaris*.

Plants of *S. vulgaris* are monocarpic (Harper and Ogden 1970). A rosette phase of vegetative growth is followed by a period of reproduction, which eventually culminates in the death of the plant. Groundsel is predominantly autogamous with outcrossing rates rarely exceeding 1% (Hull 1974). The species is a prolific seeder with 1100 to 1800 seeds per plant (Holm *et al.* 1997) and seeds are produced under a wide range of even adverse conditions (Harper and Ogden 1970). Short distance dispersal of seeds is in the range of 0 to 3 m of the motherplant (Sheldon and Burrows 1973) while occupation of new sites occurs through long distance dispersal by wind, which has not yet been quantified, or through seed transport by human activities (Frantzen and Hatcher 1997). Innate dormancy is nearly absent in *S. vulgaris* (Popay and Roberts 1970) with most seeds germinating immediately. Seeds that do not germinate have a relatively short period of survival in the soil (Roberts and Feast 1972). Seedlings emerging in autumn overwinter as a basal rosette continuing development to seed production in the following spring (Paul and Ayres 1986a). Germination is induced by light, particularly red light and is inhibited by far-red light, which is a characteristic of shade conditions (Popay and Roberts 1970). Higher nutrient levels enhance growth and reproduction of *S. vulgaris* (Aarssen and Burton 1990). Growth with respect to nutrients is also influenced by maternal effects with the growth conditions of the motherplant being reflected in the growth of the offspring

Common groundsel occurs in both ruderal and agricultural habitats. Dunes probably comprise the only natural habitat of groundsel. These coastal forms then gave rise to ruderal ones (Kadereit 1984). There are no natural habitats of *S. vulgaris* in Switzerland and it is mainly associated with ruderal habitats such as gravel pits, waste grounds and roadsides from where it likely has migrated to agricultural habitats. In the agricultural habitat it is considered as an annual weed in horticulture, orchards and plant nurseries (Holm *et al.* 1977). Groundsel was the first weed species being resistant to triazine herbicides (Ryan 1970). It is a troublesome weed if the level of herbicide resistance is high in a population and mechanical control is not feasible (Frantzen and Hatcher 1997). Under such conditions biological control might be an alternative to conventional methods of weed control.

Puccinia lagenophorae

The autoecious rust fungus *P. lagenophorae* (Uredinales, Basidomycetes) is naturally associated with *S. vulgaris*. This biotrophic fungus is one of the primary pathogens infecting groundsel (Frantzen and Hatcher 1997). Being a naturalised pathogen and an obligate parasite, not feasible for mass production, the rust is currently under investigation for the biological control of *S. vulgaris* using the system management approach (Müller-Schärer and Frantzen 1996, Frantzen and Hatcher 1997, Müller-Schärer *et al.* 2000). The fungus probably originated from Australia and was first reported in Europe in 1961 (Viennot-Bourgin 1964), where it is now common. The rust infects several Compositae such as *S. squalidus, S. vulgaris, S. viscosus, S. cruentus, Bellis perennis* and *Calendula officinalis* in Europe (Wilson *et al.* 1965). The life cycle consists of an asexual cycle, the aecidial infection and a sexual cycle, the telial infection (Fig. 1.1). However the sexual process seems to be incomplete because pycnidia and pycnidiospores have not yet been detected (Wilson *et al.* 1965). Rust infection inhibits growth and reproduction of *S. vulgaris* and increases plant mortality (Paul and Ayres 1986a,b, 1987). The higher mortality rate is attributed to secondary pathogens, which enter *S. vulgaris* plants by way of rust lesions (Hallet *et al.* 1990, Hallet and Ayres 1992). The negative impact of the rust on plants is enhanced under water stress (Paul and Ayres 1984) and well-nourished plants (Paul and Ayres 1986c). Incidence of *P. lagenophorae* is higher in autumn than in spring (Paul and Ayres 1986d) with the rust overwintering as mycelium within the host (Frantzen and Müller-Schärer 1999). Studies on the infection process of *P. lagenophorae* revealed a continuous range of variation in susceptibility of *S. vulgaris* to rust infection indicating race-nonspecific quantitative resistance (Wyss 1997, Wyss and Müller-Schärer 1999).

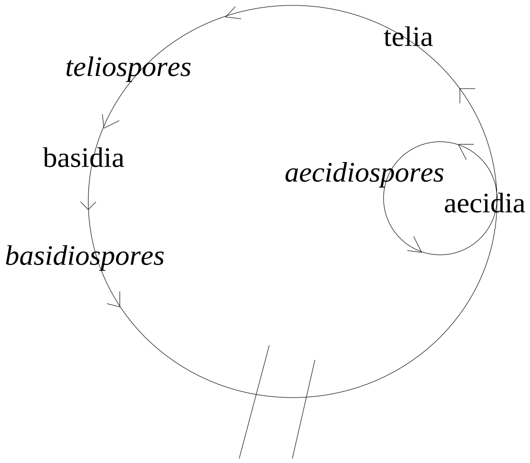


Figure 1.1 Life cycle of *P. lagenophorae* on *S. vulgaris*. Adapted from Frantzen and Müller-Schärer (1999).

Outline

A study of the population dynamics of *S. vulgaris* and *P. lagenophorae* in ruderal and agricultural habitats is presented in Chapter 2. Adaptation of *S. vulgaris* through phenotypic plasticity or genetic differentiation was assessed comparing vegetative and reproductive responses of ruderal and agricultural plants grown in the greenhouse at different nutrient and *P. lagenophorae* infection levels (Chapter 3). To establish whether differential responses of *S. vulgaris* from ruderal and agricultural habitats, detected in the greenhouse study, lead to local adaptation in the field a reciprocal seed transplant was conducted (Chapter 4). The results are integrated and discussed in Chapter 5 with respect to biological control of *S. vulgaris* in general and the use of the system management approach in particular and subsequent studies based on the results of the present thesis are proposed.

2

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

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 from April to November 1997 were conducted. 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 already appeared 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.*

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 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 propose particular weed control strategies.

Common groundsel, *Senecio vulgaris* ssp. *vulgaris* var. *vulgaris* (Asteraceae) occurs in ruderal and agricultural habitats. In the agricultural habitat it is considered as an annual weed in horticulture, orchards and plant nurseries (Holm *et al.* 1977). Dunes probably comprise the only natural habitat of groundsel. These coastal forms then gave rise to ruderal ones (Kadereit 1984). 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 likely has 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 and Hatcher 1997). Rust infection influences the fitness of *S. vulgaris* through inhibition of plant growth and reproduction as well as increased plant mortality (Paul and Ayres 1986ab, 1987a). The rust is currently investigated with respect to the biological control of *S. vulgaris* (Frantzen and 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. The study is divided into a detailed investigation at a single ruderal site focusing on spatial distribution and size variation over time, and a parallel investigation at five ruderal and agricultural sites each, investigating the dynamics of plants and rust fungus. The following specific questions were addressed: 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 2.1). 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 non-chemical measures. For comparison, 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. A population at a ruderal site, Arconciel, was selected for an 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. Number of plants and their position were determined using a counting frame of 1.1 by 1.1 m. Starting always at the same corner the frame was moved over the whole area subdividing it into 13 x 13 quadrates of 1.1 by 1.1 m. The position of each plant was precisely determined and marked by dividing a quadrate into 11 x 11 smaller quadrates of 0.1 by 0.1 m each. The whole area was initially sampled on both the 1.1 by 1.1 m and the 0.1 by 0.1 m scale. From June onwards numbers of *S. vulgaris* were too abundant to use both scales. Thus the first 6 columns of the 13 quadrates 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 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 2.1). All groundsel plants were therefore assessed at the ruderal sites. At the agricultural sites, a diagonal transect across the whole area was established and plants every 0.5 m along the diagonal were assessed. Green cover strips between crop rows were disregarded. Data were collected monthly in the period of 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

Table 2.1 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[a] Sion	waste land	5	1b Sensine	vineyard	460
2a Müntschemier	road-side	65	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

either infected by *P. lagenophorae* or not. Crop management at the agricultural sites was recorded.

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. Using plant numbers as variable it may be used as an indicator of intraspecific competition. The Moran statistic was computed as (Frantzen 1994a):

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

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 √2 referred to the eight cells adjacent to a cell. Whether the Moran statistic differed significantly from zero, i.e. a spatially random distribution, was tested by a randomisation test. Significant positive values indicate that plants are aggregated and significant negative values that plants avoid each other.

The variation of plant size within a population was expressed as the Gini coefficient (Weiner and 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):

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

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

Dynamics of ruderal and agricultural populations

Counts of *S. vulgaris* plants were analysed using hierarchical log-linear models based on the G-statistic (Sokal and 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, 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 ($P \leq 0.05$), the interaction 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 and Rohlf 1995).

Table 2.2 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 [c]	Number of dead plants [d]	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] Only plants of half the population area were marked from June onwards.
[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.

Results

Basic study

The population of *S. vulgaris* increased in number from May to July and subsequently decreased (Table 2.2). Concurrently 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 in May was in the stage of reproduction, i.e. in the stages of 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 2.3). 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.

The Moran statistic indicated a non-random, aggregated spatial pattern of *S. vulgaris* plants, except in May (Table 2.2). Considering the various developmental stages separately, plants at seed set were aggregated in May (data not presented). In July, August and September

Table 2.3 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							
<u>May-June</u>							
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
<u>June-July</u>							
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
<u>July-August</u>							
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
<u>August-September</u>							
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
<u>September-October</u>							
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.

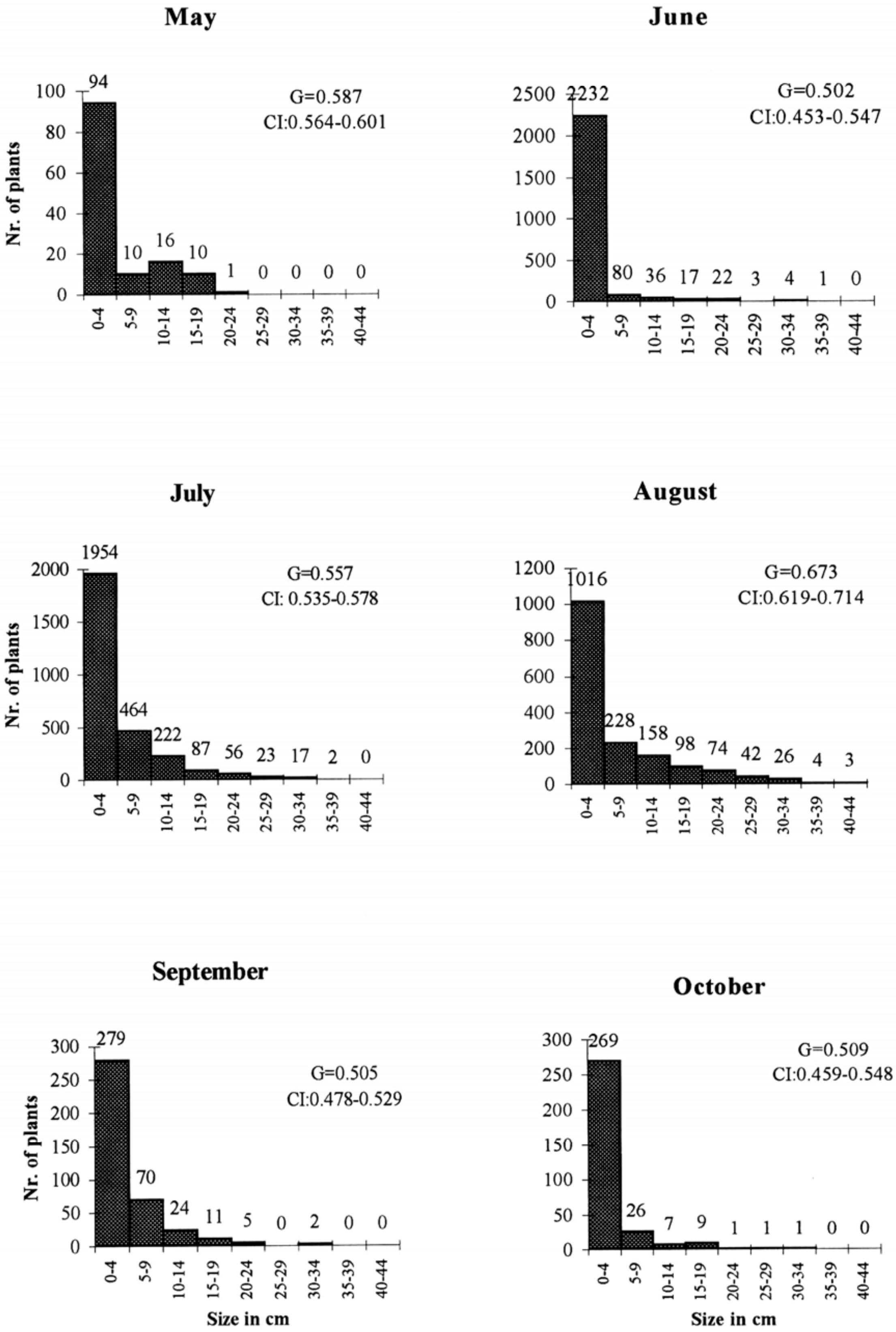


Figure 2.1 Size distributions of *S. vulgaris* expressed as the Gini coefficient (G) with a 95% confidence interval (CI) at Arconciel from May to October 1997.

Table 2.4 Significant interactions indicated by a hierarchical log-linear model[a] explaining the dynamics of *S. vulgaris* and *P. lagenophorae*.

(1) Habitat x Site x Stage x Month

(2) Habitat x Infection x Month

(3) Site x Infection x Month

(4) Habitat x Site x Stage x Infection

G = 105.8   df = 238   P = 1.000

[a] The model was fitted to counts 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).

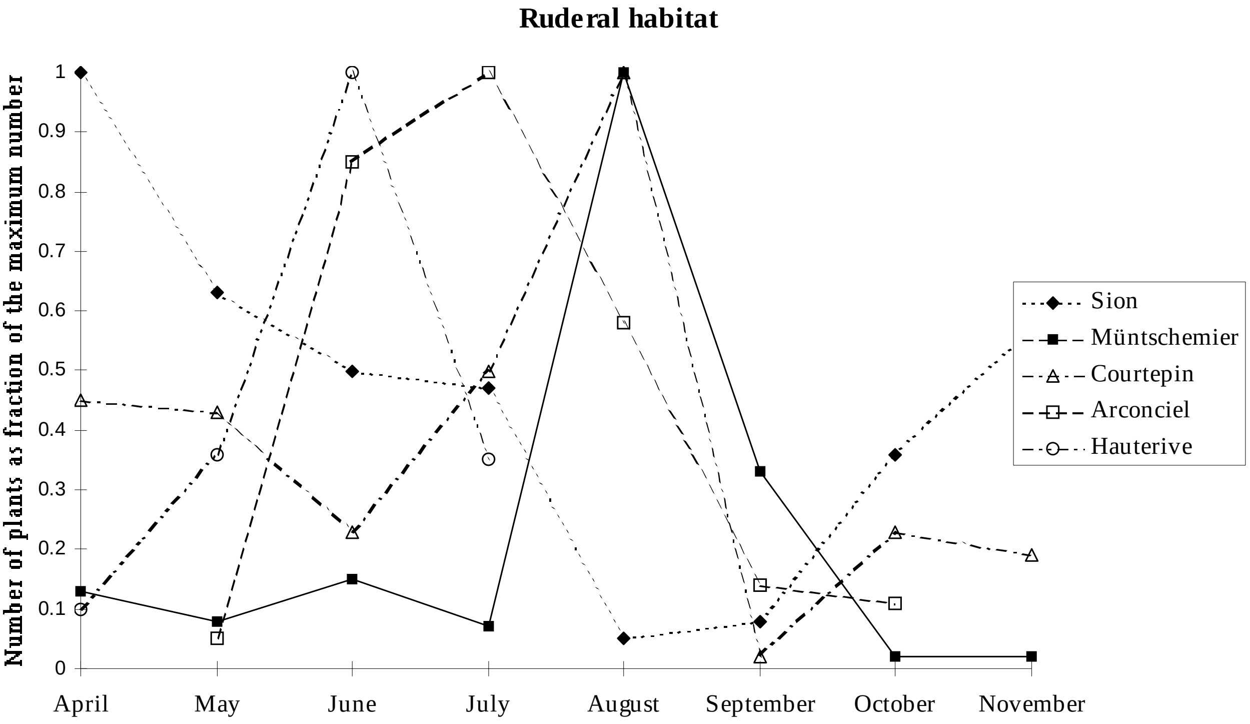
groundsel plants of all stages were aggregated, whereas in June and October some stages were not spatially aggregated (data not presented). However, analysis of the different plant stages lead to a smaller number of observations for each stage, reducing the power of the randomisation test..

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. 2.1). The Gini coefficient remained around this value, reaching a maximum in August. 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. The rust data were not analysed.

Dynamics of ruderal and agricultural populations

The analyses 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 2.4). Population dynamics of *S. vulgaris*, expressed as the variable month, differed between habitat and site as well as between plant development stage (Table 2.4, interaction 1). In April, at the begin 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. 2.2). At all sites of both the ruderal and agricultural habitat the number of *S. vulgaris* was relatively low in September. Weed control was part of the management at each 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. 2.2). Disregarding site effects a



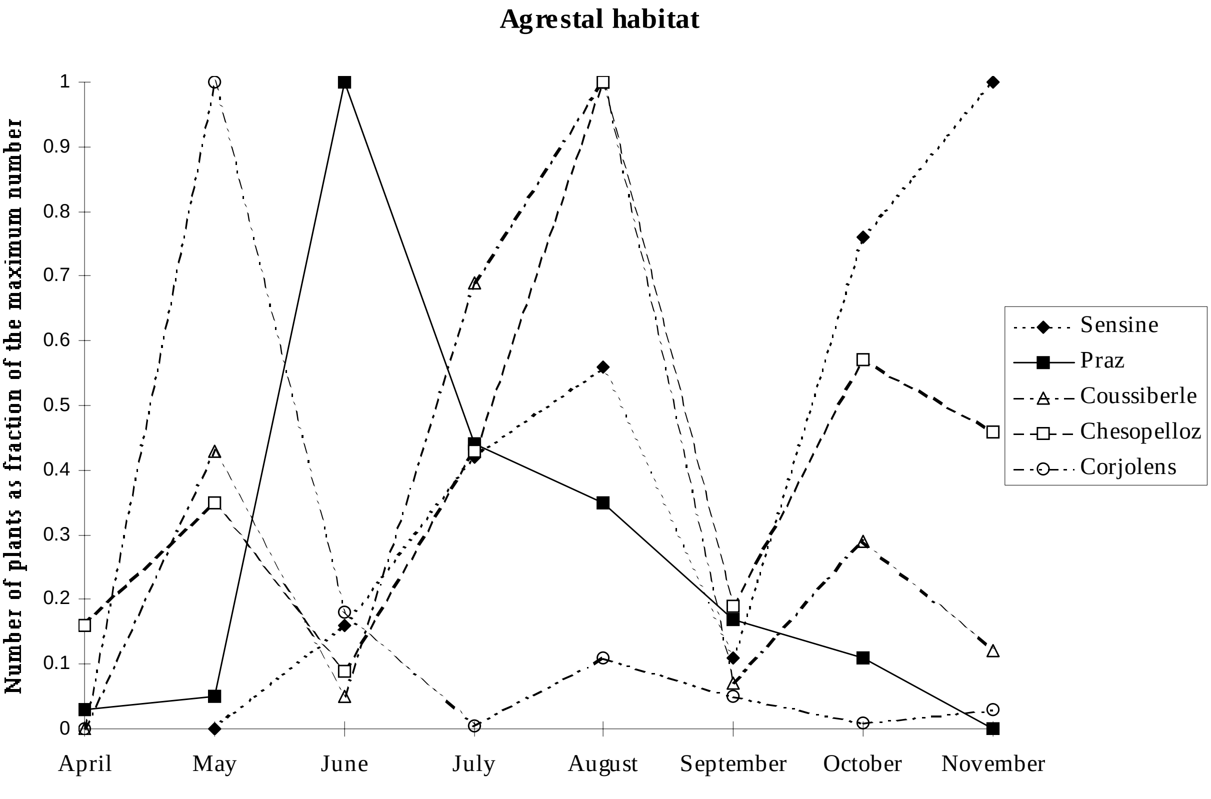


Figure 2.2 Population dynamics of *S. vulgaris* at ruderal and agricultural sites from April to November 1997. Plant numbers are expressed as fraction of the maximum number of plants determined at each site for the whole period of study. At the site of Sensine data collection started in May and at the 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.

Table 2.5 Effect of time on the plant developmental stage of *S. vulgaris* at ruderal and agricultural habitats[a].

Ruderal habitat[b]					Agricultural habitat[b]				
Month	Veget.	Bud	Flower	Seed set	Month	Veget.	Bud	Flower	Seed set
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
	$G = 2973.2$ $P \leq 0.001$[c]					$G = 438.8$ $P \leq 0.001$[c]			

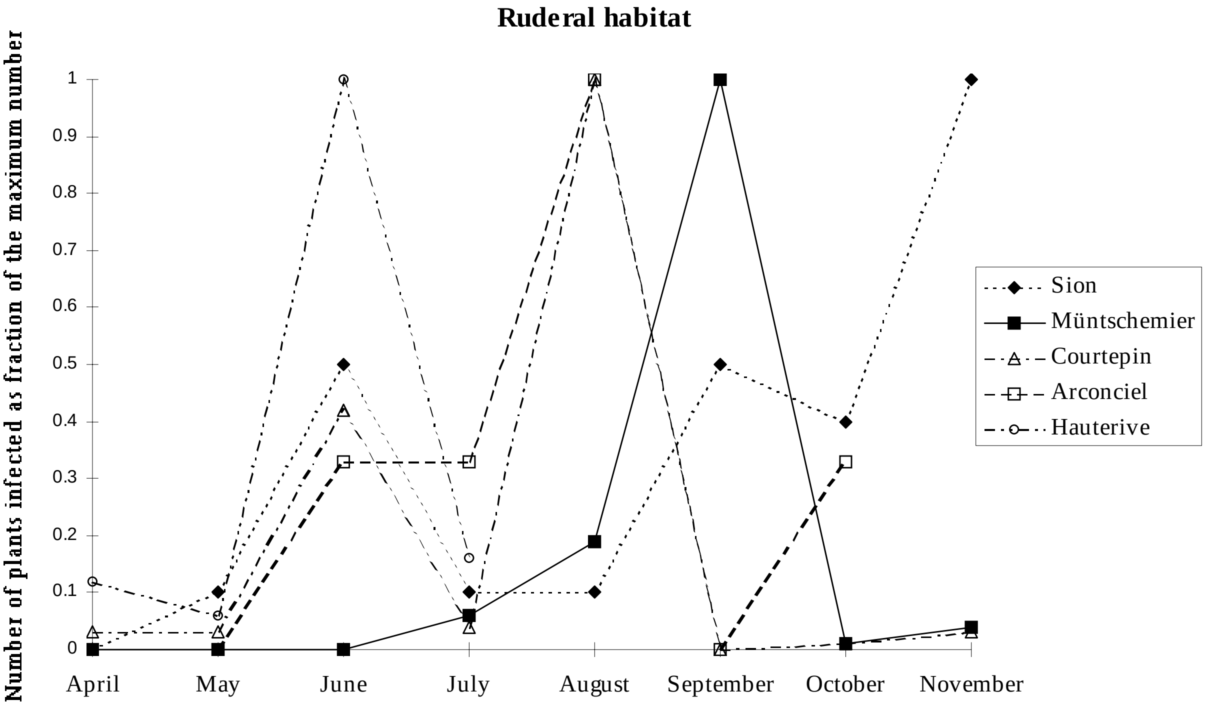
[a] Entries represent plant numbers.

[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).

significant effect of time on plant developmental stage was detected for both habitats (Table 2.5). Flowering 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 infection by month on plant numbers, differed between habitats (Table 2.4, interaction 2). The rust was abundant at the ruderal habitat from April to November, whereas at the agricultural habitat no rust was detected before August (Fig. 2.3). Independent of habitat, dynamics of *P. lagenophorae* differed between sites (Table 2.4, interaction 3). The effect of plant developmental stage on rust infection depended on habitat and site (Table 2.4, interaction 4). Disregarding site effects, a significant effect of plant developmental stage on infection was observed in both habitats (Table 2.6). 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 2.6, $P \leq 0.001$).


Ruderal habitat

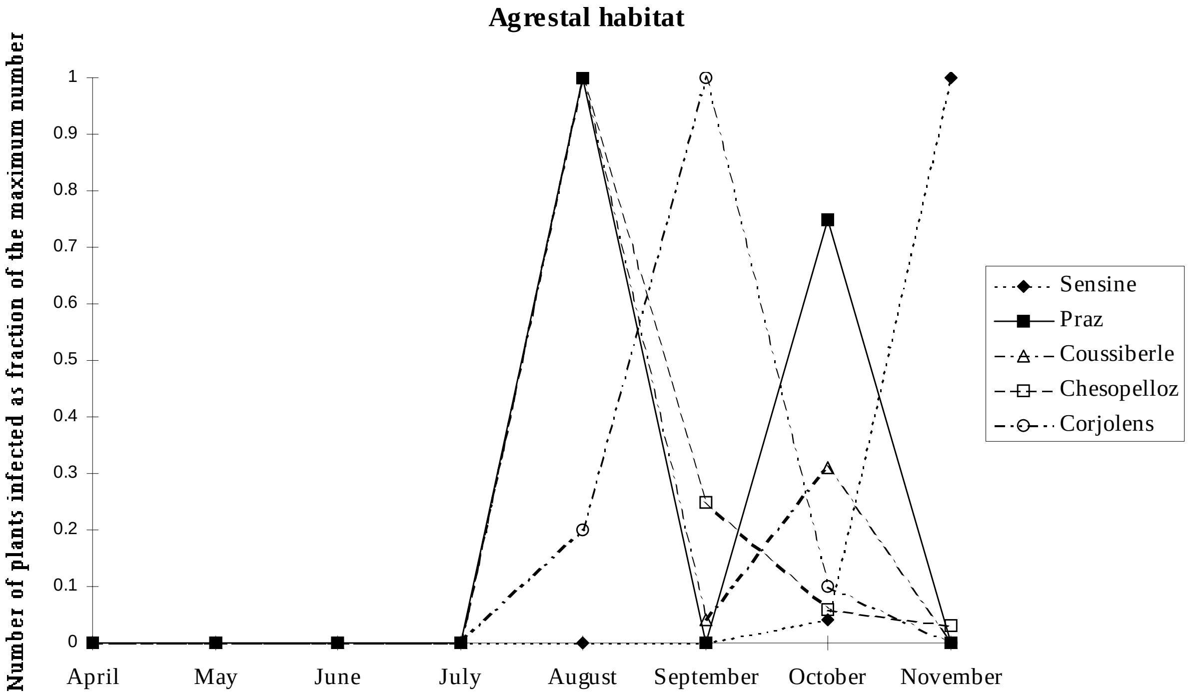

Agrestal habitat

Figure 2.3 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.

Table 2.6 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
$G = 287.4$ $P \leq 0.001$[c]			$G = 154.8$ $P \leq 0.001$[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).

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 therandom 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. 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 and 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 about seed output 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 and 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 agricultural habitat. At the ruderal habitat a major number of groundsel plants was already observed in early spring with the majority of plants in the stages of flowering or setting seed, suggesting that *S. vulgaris* plants at the ruderal habitat had wintered. 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 and Ayres 1986a). Results indicate that wintering groundsel plants with subsequent seed production in spring are a major source for the build-up of groundsel populations early in the season. Groundsel is a prolific seeder with 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 spring had to build-up either from the soil seed bank or from re-colonisation. Popay and Roberts (1970) reported innate dormancy of groundsel seeds as nearly absent. Having a low degree of innate seed dormancy, seeds that do not germinate show a relatively short period of survival in the soil (Roberts and Feast 1972). The only report of dormancy in groundsel is that of Ren and 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 not unlikely due to their morphology being 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 occurred already early in spring, while at the agricultural habitat it did not appear before August. This suggests that the rust winters as mycelium within the host at the ruderal habitat, whereas it could not survive over winter at the agricultural habitat due the relatively low number of wintering hosts. Survival of *P. lagenophorae* over winter as mycelium within plants has been demonstrated by Frantzen and 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 and 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 throughout the host development may substantially inhibit competitiveness in relation to other species (Paul and Ayres 1987b, Paul and Ayres 1989, Paul and Ayres 1990) and seed production (Paul and 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 and Frantzen 1996). A theoretical framework was developed to relate epidemics to plant competition (Frantzen and Müller-Schärer 1998), which is presently parametrised. The results of this study suggest that weed control measures at the agricultural habitat in autumn and spring result in a lack of host plants for the wintering of *P. lagenophorae* and prevent 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 and Hatcher (1997). Infected groundsel plants, which survive over winter, may serve as inoculum sources in spring inducing new rust epidemics and non-infected plants provide mature plant stages being more susceptible to rust infection enhancing rust epidemics.

The present study demonstrated that the population dynamics of *S. vulgaris* differed between the ruderal and the agricultural habitat. The difference was based on the wintering of *S. vulgaris* in the ruderal habitat leading to greater population sizes and a majority of plants in mature stages in spring compared to the agricultural habitat. The dynamics of *P. lagenophorae* also differed between habitats, being determined 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.*

Acknowledgments

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3

Adaptation of *Senecio vulgaris* to ruderal and agricultural habitats

Abstract

Adaptation of *Senecio vulgaris* to ruderal and agricultural habitats was investigated. Adaptation of plants to a habitat may occur through genetic differentiation or phenotypic plasticity. Constant inputs of fertiliser in the agricultural habitat are expected to lead to high homogeneous nutrient levels possibly causing nutrient specific differentiation of genotypes. An enhanced negative impact of the rust *Puccinia lagenophorae* on *S. vulgaris* grown at high nutrients might lead to more resistant or tolerant genotypes in the agricultural habitat. To assess adaptation of *S. vulgaris*, vegetative and reproductive responses of agricultural and ruderal plants, grown in the greenhouse at different nutrient and infection levels, were compared. Plants of *S. vulgaris* from ruderal and agricultural habitats were genetically different as indicated by a significant habitat effect. Plants from the agricultural habitat had a larger leaf area and a higher reproductive output. They also showed a stronger plastic response of reproductive traits to nutrients. It is therefore likely that genetic differentiation among habitats is nutrient specific. An increased reproductive output might be of advantage in the agricultural habitat with its disturbance due to cultivation practices. The agricultural habitat may be viewed as a group of weed patches in various crops, reminding of a meta-population, of which the sub-populations are connected by seed dispersal. Seed dispersal is improved by an increased reproductive output enabling *S. vulgaris* to quickly re-establish new patches at favourable sites. Only the agricultural habitat showed genetic diversity of *S. vulgaris*. Plasticity of reproductive characters in response to nutrients was also genetically different among families as shown by a significant family by nutrient interaction. Gene flow among the genetically different sub-populations is likely to cause the varied genotype composition of the agricultural habitat. An enhanced negative impact of the rust on plants grown at high nutrients was demonstrated, but did not lead to habitat differentiation.

Introduction

Weeds are ideal subjects for the study of adaptation and evolution due to their spread from natural or ruderal habitats into relatively recent and somewhat novel agricultural habitats (Baker 1974). Invasion of agricultural habitats followed by an increase of population size or density of the species may result in weed populations (Putwain *et al.* 1982). Understanding the adaptation of species to agricultural habitats can result in improved weed control (Jordan and Jannink 1997). Adaptation of species to a new habitat may occur in two ways: genetic differentiation or phenotypic plasticity.

It has been suggested that agricultural habitats are environmentally more homogenous than natural/ruderal habitats due to the predictability associated with tillage, crop planting and harvesting, fertiliser inputs and other environmental characteristics (Barrett 1988, Warwick 1990). Constant inputs of fertiliser in the agricultural habitat are therefore expected to lead to high homogeneous nutrient levels possibly causing nutrient specific differentiation of weed genotypes. The potential of genetic differentiation in response to increased soil nutrients levels has been shown by Snaydon (1970) and Quinn (1987). Few studies have specifically addressed genetic differentiation in response to the increased nutrient availability of agricultural habitats. Sobey (1987) reported nutrient specific differentiation of *Stellaria media* from natural and agricultural habitats, while Hermanutz and Weaver (1996) did not detect nutrient based genetic differentiation of *Solanum pthycanthum* from ruderal and agricultural habitats. The question of nutrient specific differentiation in response to increased soil nutrients levels of the agricultural habitat, still remains open.

Increasing environmental variability on a small spatial scale favours phenotypic plasticity (Bradshaw 1965, Schlichting 1986, Sultan 1987), and nutrient levels that fluctuate within a plants lifetime may lead to general-purpose genotypes (Schmid 1992, Bell *et al.* 1993). Phenotypic plasticity is therefore expected of plants in the natural/ruderal habitat in order to adapt to the heterogeneous nutrient levels of their environment. Genotypes with high levels of phenotypic plasticity as adaptation to varying nutrient levels in natural/ruderal habitats have been demonstrated (Lotz and Blom 1986, Blais and Lechowicz 1989, Sultan and Bazzaz 1993). Alternatively small-scale spatial variation may lead to differentiation of specific genotypes if selection is sufficiently intense (Slatkin 1973). Natural populations with genotypes specifically adapted to micro-sites have been reported by Abbott (1976a), Schemske (1984) and Stratton (1994, 1995).

Plants migrating from a natural/ruderal habitat to an agricultural one may thus be genotypes with high phenotypic plasticity from a population of relatively low genetic variation or specifically adapted genotypes from a population of relatively high genetic variation. In the first case most genotypes will survive in the agricultural habitat while in the second case only those genotypes will survive which derived from a micro-site with a similar environment to that of the agricultural habitat. In both cases, low genetic variation in the agricultural habitat has to be expected. In addition, genetic bottlenecks during colonisation, self-fertilisation, and selective effects of agricultural practices such as chemical weed control may have further reduced genetic variation in the agricultural habitat.

Common groundsel, *Senecio vulgaris* ssp. *vulgaris* var. *vulgaris* (Asteraceae) occurs in both ruderal and agricultural habitats. In the agricultural habitat it is considered as an annual weed in horticulture, orchards and plant nurseries (Holm *et al.* 1977). Dunes probably comprise the only natural habitat of groundsel. These coastal forms then gave rise to ruderal ones (Kadereit 1984). 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 likely has migrated to agricultural habitats. Groundsel is predominantly autogamous with outcrossing rates rarely exceeding 1% (Hull 1974). Genetic differentiation of *S. vulgaris* has been studied either by comparison of plants from various natural sites (Abbott 1976a,b) or by comparing plants from a single site (Briggs and Block 1992). Populations of *S. vulgaris* from ruderal and agricultural habitats have not been compared yet.

The rust fungus *Puccinia lagenophorae* is a primary pathogen infecting *S. vulgaris* (Frantzen and Hatcher 1997). The negative impact of the rust is enhanced on *S. vulgaris* grown at high nutrient levels (Paul and Ayres 1986c) and the impact of *P. lagenophorae* on *S. vulgaris* might be stronger in the agricultural habitat compared to the ruderal one due to the relatively high nutrient levels in the agricultural habitat. If so, *S. vulgaris* might have adapted to the stronger impact of the pathogen at the agricultural habitat by genetic differentiation into more resistant or tolerant genotypes.

Adaptation of *S. vulgaris* plants to ruderal and agricultural habitats was investigated in this study. The following specific questions were addressed: 1) Is there genetic differentiation of *S. vulgaris* between ruderal and agricultural habitats? If so, is genetic differentiation nutrient- and/or rust- specific? 2) Is there less genetic variation of *S. vulgaris* in agricultural habitats compared to ruderal habitats? To assess genetic differentiation in *S. vulgaris*, vegetative and reproductive responses of plants from ruderal and agricultural habitats, grown in the greenhouse at two nutrient and two *P. lagenophorae* infection levels, were compared.

Material and Methods

Population sampling

Five *S. vulgaris* populations each for the ruderal and the agricultural habitat type (habitat type is further referred to as habitat) were sampled in the districts Fribourg and Valais of Switzerland in October 1996. The agricultural populations comprised annual and perennial crops (Table 3.1). The largest distance between any two populations was 86 km and the shortest 3 km. Seeds of each of five randomly chosen plants were collected from each population and one seed family per plant was established. To minimise maternal effects seed families were grown for one generation in a heated greenhouse, selfed and the resulting seeds used in the experiment.

Table 3.1 Ruderal and agricultural populations used for sampling of *S. vulgaris* from ruderal and agricultural habitats.

Ruderal habitat		Agricultural habitat	
Location	Description	Location	Description
Sion	waste land	Conthey	apple orchard
Arconciel	gravel pit	Chesopelloz	apple orchard
Sugiez	waste land	Praz	vineyard
Rosè	waste land	Corjolens	vegetables
Courtepin	waste land	Coussiberle	vegetables

Experimental treatments

Of each family separately, four seeds were sown into 9 cm diameter pots filled with TKS 1 Floragard® peat substrate. Seeds were moistened three and six days after sowing using a de Vilbiss sprayer. The first emerging seedling of each pot was used for the experiment while the other emerging seedlings were removed. A single pot per family and treatment was allocated to each of three greenhouse benches in a randomised complete block design without repetition (i.e. 4 pots/family/treatment level, for a total of 600 pots). Two treatments with two levels each were applied. The first treatment comprised addition or not of nutrients in form of the slow release fertiliser Tardit Top® mixed into the peat substrate at potting. Plants with the nutrient treatment received 4 g/l 14-7-14 NPK with the total amount of nutrients applied corresponding to a field application rate of 366 kg ha $^{-1}$ nitrogen and potassium respectively, and 183 kg ha $^{-1}$ phosphate. The second treatment consisted of inoculation or not with the rust fungus *P. lagenophorae*. The rust line used was collected from a ruderal *S. vulgaris* population at Unterehrendingen in Switzerland. Inoculation took place when the majority of plants had four leaves apart from the cotyledons. A suspension of 75 mg *P. lagenophorae* aeciospores in 150 ml H_2O served as inoculum and was applied with a de Vilbiss sprayer. Plants were covered with plastic bags after inoculation to allow for a 12 h dew period. To standardise treatments non-inoculated plants were also covered with plastic bags. A second inoculation was carried out one week later. Pots were watered from below to insure consistent soil moisture. Plants were treated once with a 0.5% Teknar® solution to control *Sciarid* fly larvae. Relative humidity varied from an average of 59% at day to 83% at night. Plants were grown at an average temperature of 24 C° over day with a maximum of 38 C° on sunny days and 19 C° during night. Incident light was supplemented by high pressure ionised lamps (type SGR, Philips Son-T-400W) to provide 16 h daylight. Light intensity reached 199 µmol m^{-2} s^{-1} on average with a maximum of 1002 µmol m^{-2} s^{-1}on sunny days. The experiment was conducted in the period 3 September to 22 November 1997. Plants were harvested individually when the first capitulum matured, i.e. at first seed set. Seventeen plants died in the course of the experiment independent of treatment.

Measurements

Various vegetative and reproductive characters were measured. All characters, except time to cotyledon formation, were measured at harvest. Vegetative characters comprised time to formation of cotyledons, average leaf area of the third and fourth leaf being determined by image analysis (NIH Scion Image 1.57) and vegetative biomass expressed as dry weight of stems and leaves. Reproductive characters included time to first seed set, number of seeds in the first maturing capitulum, number of capitula and reproductive biomass expressed as the sum of the dry weight of seeds in the first maturing capitulum, capitula and flower buds. Severity of rust infection was determined for the third and fourth leaf using image analysis (NIH Scion Image 1.57).

Data analysis

Data were analysed with a three level nested ANOVA with habitat, population nested within habitat and family nested within population. A mixed model was applied with block, habitat, nutrients and rust considered as fixed main factors. Populations and families were randomly sampled and therefore population as well as family and consequently their interactions with treatments were considered as random effects. Block used the error mean square as the denominator for significance tests. Habitat, population, family and their interactions with treatments were tested against the corresponding next lower hierarchical level (Sokal and Rohlf 1995). Treatments and their interactions used population by treatments as the error term. A significant habitat, population or family effect indicate constant differences in mean performance across environments and thus genetic differences. A significant habitat-, population-, or family by treatment interaction term indicates genetic variation of phenotypic plasticity.

Characters with a significant habitat by treatment interaction were further analysed by separate two level nested ANOVAs (population and family nested within population) for each habitat. Appropriate error terms were as for the three level ANOVA excluding the habitat factor.

The overall plastic response of ruderal and agricultural plants to variation in nutrients and rust infection was evaluated by canonical discriminant analysis (Manly 1994). Each of the habitat-nutrient and habitat-rust combinations was treated as a group in the analysis. All vegetative and reproductive characters were used to characterise each plant in this multivariate comparison. Distances between group centroids were measured by Mahalanobis distance, which may be used as a measure of total amount of plasticity (Zhang and Lechowicz 1994), and tested using a F-ratio (Manly 1994).

Results

Vegetative and reproductive characters of *S. vulgaris* differed significantly between habitats, nutrient and rust treatments (Table 3.2). Number of capitula and reproductive biomass were characters affected by all three factors. No effects of these factors on number of seeds in the first maturing capitulum could be detected. Leaf area was genetically different among habitats with on average 5.41 cm^2 in the ruderal and 7.61 cm^2 in the agricultural habitat and increased significantly with addition of nutrients. Plants from the agricultural habitat produced a higher number of capitula and an increased amount of reproductive biomass compared to those from the ruderal habitat (Table 3.3). As expressed by the significant habitat by nutrient interactions (Table 3.2) additional nutrients lead to a significantly higher increase in number of capitula and reproductive biomass in the agricultural habitat compared to the ruderal one (Fig. 3.1). Genetic differences among families for both number of capitula and reproductive biomass were only detected for the agricultural habitat (Table 3.4). Agricultural families differed significantly in their reaction towards nutrient application (Fig 3.1) as indicated by the significant family by nutrient interaction (Table 3.4).

Rust infection significantly decreased leaf area, vegetative biomass, number of capitula and reproductive biomass (Table 3.3). The response of reproductive characters to rust infection did not differ between habitats. Differences in the response of reproductive characters to rust infection were detected at the population level (Table 3.2) and here only among ruderal populations (Table 3.4). Plants with additional nutrient application showed a stronger response to rust infection as expressed by significant nutrient by rust interactions for vegetative biomass (Table 3.2) and number of capitula (Table 3.4).

Plants of *S. vulgaris* from ruderal and agricultural habitats could be distinguished by canonical discriminant analysis (Fig. 3.2). The first two axes of the two dimensional canonical graph accounted for 93% of the variance among groups. The first canonical axis separated the groups with and without additional nutrients, while the second axis separated habitats. Separation into habitats was more evident for plants with nutrient application. Separation of nutrient groups was strongest due to vegetative biomass, (largest canonical discriminant function coefficient for function 1 = 1.038) while habitats were separated best by reproductive biomass (largest canonical discriminant function coefficient for function 2 = 1.144). The third canonical axis separated the groups with and without rust infection. It only explained 6% of the variance among groups and was therefore omitted from the graph for simplicity. Analysis of Mahalanobis distances confirmed that groups were significantly different (Table 3.5). The distance between groups with and without nutrient application in the agricultural habitat was

Table 3.2 Nested ANOVA for vegetative and reproductive characters of *S. vulgaris* from ruderal and agricultural habitats in response to nutrient application (N) and rust infection (R). Mean squares and significance levels are presented.

	df	Time cotyledons	Leaf area	Vegetative biomass	Time seed set	Number of capitula	Number of seeds	Reproductive biomass
Block	2	1433.515***	95.512***	0.462 ns	1610.065***	1449.039*	1118.652***	0.065 ns
Habitat	1	6.925 ns	605.888*	0.479 ns	192.116 ns	32096.160**	702.857 ns	1.331**
Population(in habitat)	8	153.219*	91.438***	2.389*	273.509**	2913.516*	1372.697**	0.084 ns
Family (in population)	40	59.306***	20.757***	0.946***	95.984***	1099.046 ***	411.378***	0.052**
N	1	1618.109***	1376.258***	352.711***	1834.203***	239583.057***	115.290 ns	8.275***
R	1	12.920 ns	88.023 ***	27.981***	142.494ns	40255.891***	267.272 ns	4.025***
N x R	1	25.136 ns	28.263 ns	8.283***	125.600 ns	2374.238 ns	9.843 ns	0.065 ns
Habitat x N	1	25.531 ns	5.022 ns	0.096 ns	18.465 ns	10954.009*	34.299 ns	0.444*
Habitat x R	1	0.251 ns	0.315 ns	0.070 ns	0.015 ns	5.799 ns	5.380 ns	0.003 ns
Habitat x N x R	1	10.747 ns	1.250 ns	0.009 ns	89.104 ns	10.404 ns	95.998 ns	0.020 ns
Population x N	8	6.573 ns	36.623***	1.492**	37.987 ns	1644.046 ns	82.471 ns	0.051 ns
Population x R	8	18.364 ns	16.436 ns	0.307 ns	51.704 ns	774.370 ns	77.007 ns	0.062 **
Population x N x R	8	25.755 ns	5.922 ns	0.205 ns	58.088 ns	473.663 ns	63.231 ns	0.021 ns
Family x N	40	14.061 ns	7.677 ns	0.509**	26.135 ns	751.664*	148.474 ns	0.041*
Family x R	40	19.772 ns	8.783 ns	0.321 ns	32.253 ns	424.023 ns	168.879 ns	0.019 ns
Family x N x R	40	21.051 ns	8.686 ns	0.258 ns	41.852 ns	367.523 ns	158.252 ns	0.023 ns

*$p \le 0.05$, **$p \le 0.01$, *** $p \le 0.001$, ns non significant

Table 3.3 Means and standard errors of reproductive characters of *S. vulgaris* from ruderal and agricultural habitats in response to nutrient application (+N/-N) and rust infection (+R/-R). Entries are based on 25 families per habitat replicated 3 times.

	Ruderal habitat				Agricultural habitat			
	- N	+ N	- R	+ R	- N	+ N	- R	+ R
Number of capitula	35.84 ± 1.48	71.42 ± 2.58	35.84 ± 1.48	23.05 ± 1.39	41.75 ± 1.61	95.52 ± 4.27	41.75 ± 1.61	29.29 ± 1.75
Reprod. biomass (g)	0.31 ± 0.01	0.53 ± 0.02	0.31 ± 0.01	0.18 ± 0.01	0.37 ± 0.01	0.67 ± 0.03	0.37 ± 0.01	0.21 ± 0.01

higher than that for the ruderal habitat, indicating a stronger overall plastic response to nutrients in the agricultural habitat (Table 3.5A). Overall phenotypic plasticity to rust infection was substantially lower than that to nutrient application (Table 3.5B). The distance between groups with and without rust infection in the agricultural habitat was only slightly higher than that for the ruderal habitat, indicating that plants from both habitats had a similar amount of plastic response to rust infection.

Discussion

Plants of *S. vulgaris* from ruderal and agricultural habitats were genetically different as indicated by a significant habitat effect. Plants from the agricultural habitat had a larger leaf area and a higher reproductive output, which might be sustained by the larger leaf area available for photosynthesis. The increased reproductive output was expressed in an increased number of capitula and reproductive biomass, compared to plants from the ruderal habitat. Habitats also differed in the genetic variation of reproduction in response to nutrients. Plants from the agricultural habitat showed a stronger plastic response to nutrient addition compared to the ruderal ones. It therefore seems likely that the genetic differentiation of reproductive traits among habitats is nutrient specific. Agricultural habitats have higher levels of nutrients due to constant fertilisation, and plants of these habitats seem to be able to translate these higher nutrient levels into an increased reproductive output.

Results are in contrast to the study of Hermanutz and Weaver (1996) comparing *Solanum ptycanthum* of ruderal and agricultural habitats. They neither detected genetic differences associated with nutrient availability nor divergence in the amount of overall plasticity to nutrients. Also Blais and Lechowicz (1989) did not detect genetic differentiation of *Xanthium strumarium* from nutrient-rich natural and nutrient-poor ruderal habitats but they reported differences in the overall plastic response to nutrient availability between habitats. Sobey (1987), comparing *Stellaria media* from natural and agricultural habitats, obtained results similar to those of this study. Plants of the two habitats were genetically different, with plants from the agricultural habitat having a higher seed output. Plants of the agricultural habitat also showed a higher increase of seed output at high soil fertility compared to plants of the natural habitat. Greater production of seed at the high soil fertility level was based on an

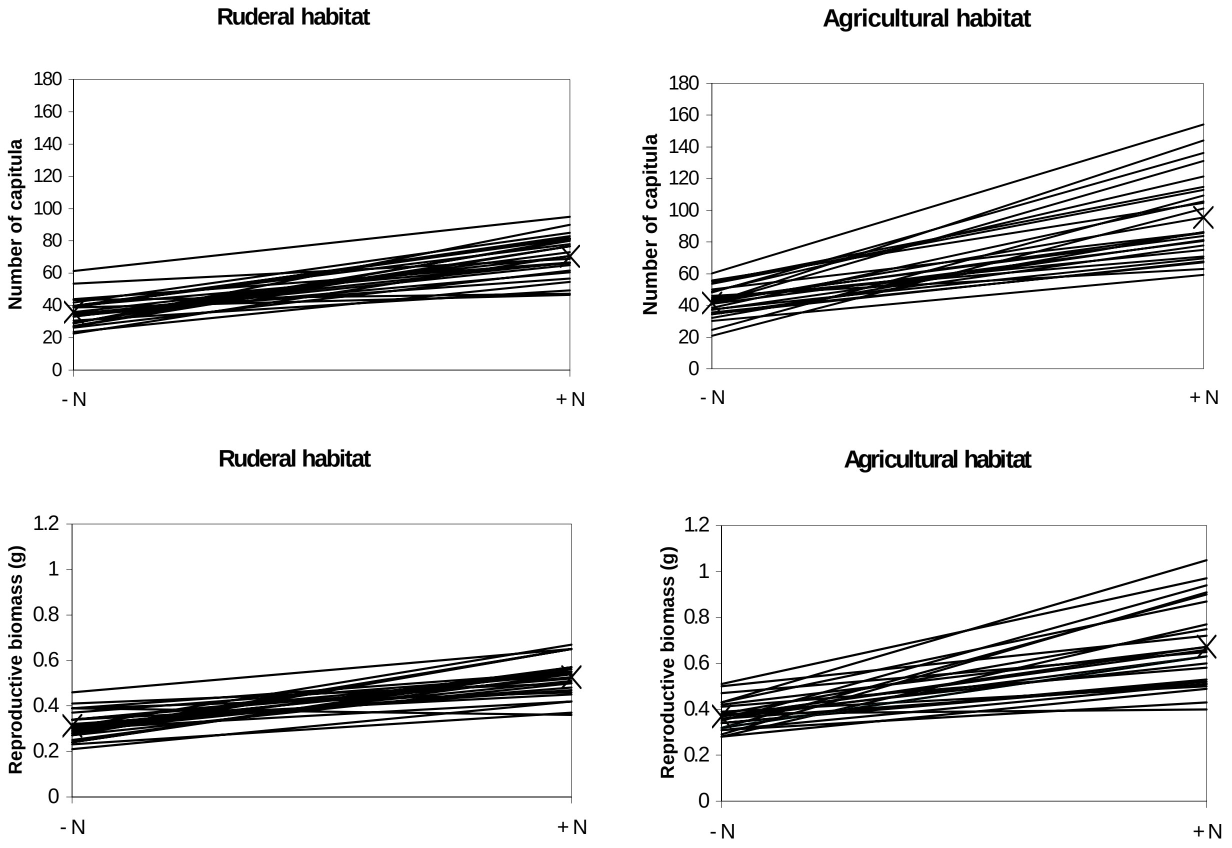

Figure 3.1 Reaction norms of *S. vulgaris* from ruderal and agricultural habitats grown with (+N) and without (-N) additional nutrients. The mean reaction norm is indicated by x.

earlier onset of reproduction, with the short pre-reproductive period being an adaptation to the high risk of mortality in the agricultural habitat caused by regular disturbance due to cultivation practices. In the present study no differences in the onset of reproduction between *S. vulgaris* from ruderal and agricultural habitats could be detected, although a shorter generation time for *S. vulgaris* from intensively weeded sites in a botanic garden in comparison to less intensively or non weeded sites has been reported (Kadereit and Briggs 1985, Briggs and Block 1992).

Following a different strategy than an early onset of reproduction an increased reproductive output might also be of advantage for *S. vulgaris* in the regularly disturbed agricultural habitat. Seeds of *S. vulgaris* have a low degree of innate dormancy and seeds that do not germinate show a relatively short period of survival in the soil (Popay and Roberts1970, Roberts and Feast 1972). With the soil seed bank being of minor importance, re-establishment of agricultural *S. vulgaris* populations may occur through colonisation, requiring dispersal of *S. vulgaris* seeds from adjacent field margins or neighbouring crops and dispersal of agricultural *S. vulgaris* plants may be enhanced by increased fecundity. If so, the agricultural habitat might be viewed as a group of weed patches in various crops reminding of a meta-population of which the sub-populations are connected by seed dispersal (Cousens and Mortimer 1995). In this context the agricultural habitat is a highly variable and unpredictable environment due to crop rotation and variation in timing of cultivation practices. Translation of higher nutrient levels into increased fecundity, through a higher seed output, seems to be an

Table 3.4 Nested ANOVA per habitat for reproductive characters of *S. vulgaris* from ruderal and agricultural habitats in response to nutrient application (N) and rust infection (R). Mean squares and significance levels are presented.

		Ruderal habitat		Agricultural habitat	
	df	Number of capitula	Reproductive biomass	Number of capitula	Reproductive biomass
Block	2	1019.730 ns	0.003 ns	1413.564 ns	0.095 ns
Population	4	322.191 ns	0.014 ns	5518.972 ns	0.155 ns
Family (in population)	20	323.892 ns	0.018 ns	1881.647***	0.086***
N	1	73895.389***	2.463**	175836.607***	6.213***
R	1	19611.077**	1.912**	21010.421**	2.143**
N x R	1	1027.160*	0.079 ns	1359.091 ns	0.007 ns
Population x N	4	918.630*	0.046**	2361.218 ns	0.055 ns
Population x R	4	868.277*	0.055*	702.277 ns	0.072 ns
Population x N x R	4	98.803 ns	0.014 ns	863.026 ns	0.029ns
Family x N	20	240.257 ns	0.010 ns	1260.670**	0.073**
Family x R	20	217.863 ns	0.013 ns	626.943 ns	0.025 ns
Family x N x R	20	223.341 ns	0.011 ns	515.866 ns	0.036 ns

$^*p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$, ns non significant

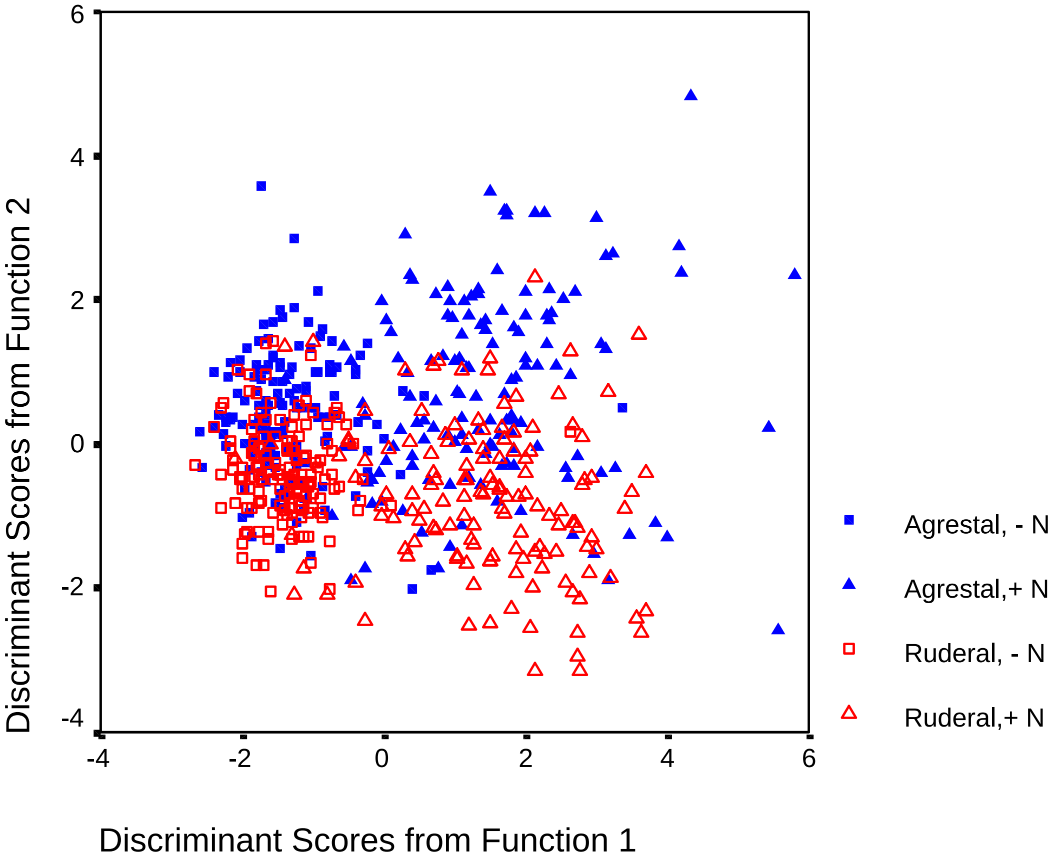

Fig 3.2 Canonical discriminant analysis separating *S. vulgaris* from ruderal and agricultural habitats grown at two nutrient and two rust levels. The graph displays the first two canonical axes only. The third canonical axis, separating the groups with and without rust infection, only explained 6% of the variance among groups and was therefore omitted for simplicity.

adaptation of *S. vulgaris* plants to this heterogeneity enabling them to quickly re-establish new patches at favourable sites.

Contrary to expectations it was the agricultural habitat that showed genetic diversity of *S. vulgaris* and not the ruderal one. Families differed in reproductive characters and also plasticity of reproductive characters in response to nutrients was genetically different among families as indicated by a significant family by nutrient interaction. Looking at the agricultural habitat as a generally larger habitat compared to the ruderal one and consisting of a group of weed patches in various crops reminding of a meta-population, nutrient levels within the agricultural habitat will be different. The more varied genotype composition in the agricultural habitat is therefore likely to be caused by gene flow among sub-populations adapted to sites with different levels of nutrients within the habitat.

Genetic differentiation between habitats based on rust infection could not be detected, although populations within the ruderal habitat showed genetically different responses to rust infection. Results of Paul and Ayres (1986c) demonstrating an enhanced negative impact of the rust on *S. vulgaris* grown at high nutrient levels were supported. However, the enhanced negative impact of the rust on well-nourished plants did not seem to be strong enough to lead to differentiation between habitats. Additional data are required to substantiate the idea of genetic differentiation of *S. vulgaris* in response to the stronger impact of the pathogen at the

Table 3.5 Mahalanobis distances of the canonical discriminant analysis separating *S. vulgaris* from ruderal and agricultural habitats grown (**A**) with (+) and without (-) additional nutrients and (**B**) with (+) and without (-) rust infection. Significant differences among groups were tested using a F ratio.

A

	Ruderal/ + Nutrients	Ruderal/ - Nutrients	Agricultural/ + Nutrients	Agricultural/ - Nutrients
Ruderal/+ Nutrients	-			
Ruderal/- Nutrients	8.586***	-		
Agricultural/+ Nutrients	5.959***	14.586***	-	
Agricultural/- Nutrients	11.837***	1.181***	14.383***	-

*** P ≤ 0.001

B

	Ruderal/ /+ Rust	Ruderal/ / - Rust	Agricultural/ /+ Rust	Agricultural/ / - Rust
Ruderal/+ Rust	-			
Ruderal/- Rust	0.965***	-		
Agricultural/+ Rust	0.923***	1.360***	-	
Agricultural/- Rust	1.360***	1.181***	2.319***	-

*** P ≤ 0.001

agricultural habitat.

Colonising the agricultural habitat *S. vulgaris* seems to have adapted to the higher nutrient levels of the this habitat by genetic differentiation of genotypes with a high phenotypic plasticity in response to nutrients. These genotypes are able to translate high nutrient levels into high reproductive biomass. However, the genetic composition of genotypes in the agricultural habitat is more varied also comprising genotypes with a relatively low response to high nutrient levels. The present study suggests that although nutrient levels in the agricultural habitat are higher they are not as homogenous as generally proposed and that the more varied genotype composition is caused by gene flow among sub-populations adapted to sites with different levels of nutrients. Thus the agricultural habitat is not genetically impoverished as often supposed but shows higher genetic diversity than the ruderal habitat.

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4

Demography of reciprocally sown populations of *Senecio vulgaris* from ruderal and agricultural habitats

Abstract

Colonising crop fields *Senecio vulgaris* from ruderal habitats may persist in the new environment through phenotypic plasticity or genetic differentiation. Differential response of life history traits to selection may lead to local adaptation. A reciprocal seed transplant experiment was conducted to determine environmental and genetic variation of life history traits in *S. vulgaris* from ruderal and agricultural habitats and whether infection by the rust *Puccinia lagenophorae* is a selection factor in *S. vulgaris* populations. Emergence, growth and fecundity showed environmental as well as genetic variation. However, there was no evidence of local adaptation as indicated by the absence of significant origin by site interactions. Genetic variation of emerging seedling numbers seems to be important for *S. vulgaris* as an annual plant. Seedling survival was solely under environmental control stressing the importance of stochastic events for plant mortality. Most *S. vulgaris* from ruderal sites showed reduced growth, but still reached reproduction, suggesting that *S. vulgaris* can endure unfavourable environments reducing vigour following the strategy of a stress tolerator. Plants at most agricultural sites behaved like r-strategists exploiting a productive environment for rapid plant growth maximising reproduction. Emergence, survival growth and fecundity were higher at the agricultural sites. Infection by the rust occurred at all sites, with the highest incidence at the agricultural sites, and was solely determined by the environment. A higher incidence did not result in an increased disease impact nor did it affect survival of *S. vulgaris*. With all other life history traits supporting the prerequisites of natural selection it is likely that stochastic environmental events during the experiment may have obscured adaptation and that in the absence of stochastic mortality *S. vulgaris* has the potential to adapt to its local environment.

Introduction

Plants from ruderal habitats colonising crop fields face new environmental challenges. Agricultural habitats differ from natural/ruderal habitats due to human activity comprising tillage, crop planting and harvesting, fertiliser inputs, weed control and other cultivation practices. The colonising species may nevertheless increase in population size or density and result in weed populations (Putwain *et al.* 1982). Persistence of the colonising species may occur through phenotypic plasticity or genetic differentiation. In the presence of genetic variation, differential response of life history traits to selection may lead to local adaptation and result in habitat-related life history differences of the coloniser (Rice and Mack 1991).

Selection may vary among life history traits (McGraw and Antonovics 1983, Schmidt and Levin 1985) with emergence, survival, growth and fecundity being the determinant components of plant life histories. It is therefore important to study the complete plant life cycle with respect to selection (Van Groenendael 1985). However, relatively few evolutionary studies included all plant life cycle components like the studies conducted by Levin and Schmidt (1985), Schmidt and Levin (1985), Cheplick (1988) and Rice and Mack (1991). Especially emergence and growth at early stages are often not studied although the importance of events occurring at the seedling stage on plant fitness has been emphasised (Harper 1977).

The reciprocal transplant technique is considered as the classical method for the analysis of variation in life history traits and the adaptive significance of genetic differentiation (Rapson and Wilson 1988, Schmid 1992). If resident individuals consistently outperform the alien individuals in terms of emergence, survival, growth and fecundity, then this can be accepted as evidence for natural selection and evolutionary adaptation to local conditions (Primack and Kang 1989). Genetic differences between populations may also be demonstrated with greenhouse or common garden experiments. However, such experiments do not directly address the potential adaptive nature of genetic variation (Rice and Mack 1991). Antonovics and Primack (1982) argued that field transplants lead to a more realistic assessment of genetic and environmental effects, because they also include biotic factors which might be important for the development of localised adaptations.

We conducted a reciprocal seed transplant experiment to determine the influence of environmental and genetic effects on life history traits of *S. vulgaris* from ruderal and agricultural habitats. Common groundsel, *Senecio vulgaris* ssp. *vulgaris* var. *vulgaris* (Asteraceae) occurs in both ruderal and agricultural habitats. It is considered an annual weed in horticulture, orchards and plant nurseries (Holm *et al.* 1977). Dunes probably comprise the only natural habitat of groundsel. These coastal forms then gave rise to ruderal ones (Kadereit 1984). 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 road-sides from where it likely has migrated to agricultural habitats. Groundsel is predominantly autogamous with outcrossing rates rarely exceeding 1% (Hull 1974). The autoecious rust fungus *Puccinia lagenophorae* is naturally associated with *S. vulgaris*. This biotrophic fungus is one of the primary pathogens infecting groundsel (Frantzen and Hatcher 1997). Rust infection affects the fitness of *S. vulgaris* by a negative impact on plant growth and reproduction as well as causing an increased plant mortality (Paul and Ayres 1986ab, 1987a). The higher mortality rate is attributed to secondary pathogens, which enter *S. vulgaris* plants by way of rust lesions (Hallet *et al.* 1990, Hallet and Ayres 1992). Rust infection is thus a potential selection factor to which *S. vulgaris* may adapt. Responses of plant fitness parameters to pathogen infection have so far not been included in reciprocal transplant studies.

We specifically addressed the following questions i) Are the life history traits emergence, survival, growth and fecundity in *S. vulgaris* determined by environmental and/or genetic variation? ii) Are life histories of ruderal and agricultural *S. vulgaris* adapted to their local environment and if so, does adaptation occur for each trait? iii) Is the rust fungus *P. lagenophorae* an important biotic factor with respect to the local adaptation of *S. vulgaris*?

Material and methods

Field sites

Three *S. vulgaris* populations each for the ruderal and the agricultural habitat type were sampled in the district Fribourg of Switzerland in October 1996 and April 1997. The largest distance between any two populations was 24 km and the shortest 3 km. Seeds of each of five randomly chosen plants were collected from each population and one seed family per plant was established. To minimise maternal effects seed families were grown for one generation in a heated greenhouse, selfed and the resulting seeds were sown at the same sampling sites. The sites were:

Arconciel: an area of 13 by 13 m in a gravel pit on a stony ground of sandy loam. *S. vulgaris* is a major component of the vegetation, which is dominated by *Tussilago farfara* and *Trifolium repens*.
Courtepin: a waste ground of 5 by 18 m with a compacted, shallow sandy soil, which quickly drains. Vegetation is sparse with *S. vulgaris*, *Conyza canadensis* and *Eragrostis minor* being the main components.
Müntschemier: an area of 3 by 22 m on top of a road-shoulder. The soil is a compacted sandy loam with slow drainage. *S. vulgaris* is a minor component of the vegetation, being dominated by *Trifolium repens* and *Polygonum avicolare*.
Coussiberle: a vegetable plot with cabbage of 4.5 by 60 m size. The soil is a sandy loam. The site is regularly fertilised and watered sporadically.
Corjolens: a vegetable plot with leek of 4 by 25 m size. The soil is a sandy loam. The site is regularly fertilised and irrigated.
Praz: a vineyard situated in a plane of about 3800 m^2 on sandy loam. The site is regularly fertilised but not irrigated.

Reciprocal seed transplant experiment

Seeds of each origin were sown into a 1.50 by 6.00 m plot established at each site. Each plot contained six replicated seeds with 6 sites x 6 origins x 5 families x 6 replicates amounting to a total of 1080 seeds per site. Germination of *S. vulgaris* is induced by light and can be inhibited under shade conditions (Frantzen and Hatcher 1997 and reference therein). To facilitate germination and to prevent contamination with invading *S. vulgaris* seeds the vegetation in all plots was removed prior to sowing, plots were regularly weeded and seeds were placed on pieces of 2% water agar, which then were placed into each plot depositing them into a small cavity. This method was developed by Kempenaar and Schnieders (1995) to obtain sufficient emergence of *S. vulgaris* for field experiments. Three replicated seeds were placed on a piece of water agar of approximately 1 by 1 cm size. The first emerging seedling on a piece was used for the experiment while the other emerging seedlings were removed. Seeds were marked with numbered sticks for identification. During the first week after sowing plots were protected by gauze and seeds were moistened through the gauze using a knapsack sprayer to prevent desiccation. Throughout the experiment plots were protected with a coarse net, at about 1 m height, to exclude disturbance by humans and animals. Every fortnight Limax ® (3.5% Metaldehyde) granules were applied to control slugs. Plants were harvested individually at the onset of reproduction when the first capitulum matured i.e. at first seed set. The experiment was conducted in the period from 6 August to 16 November 1998.

Measurements

Various characters were measured twice a week starting one week after sowing: emergence of seedlings (unfolding of cotyledons), plant survival, plant height (length in cm from the base of the plant to the terminal apical meristem) and rust infection (yes or no). Several vegetative and reproductive characters were measured at harvest: average leaf area of the third and fourth leaf (determined by image analysis, NIH Scion Image 1.57), above ground biomass (dry weight in mg), time to the onset of reproduction, plant height at onset of reproduction and number of capitula. Severity of rust infection was determined as the fraction of area infected of the third and fourth leaf using image analysis (NIH Scion Image 1.57).

Data analysis

Data analysis was based on the effects of origin, representing genetic variation and site, representing environmental variation. The interaction between origin and site suggests local adaptation (Van Groenendael 1985).

Emergence of seedlings, survival to reproduction and rust incidence were analysed by logistic regression based on individual plants. Significance of effects was estimated with the Wald test (Hosmer and Lemeshow 1989). The origin or site with the lowest value was chosen as the reference independent variable for calculation of the odds ratio. In this case the odds ratio is the multiplicative factor that describes the increase in the probability of an event (i.e. emergence, survival, rust incidence) when the independent variable increases by one unit.

Growth curves were fitted by non-linear regression, fitting log-logistic curves (Frantzen 1994b):

$$y = 1/[1(1+exp(-b*ln(t/\tau)))],$$

where y = the fraction of plant height at onset of reproduction, b = a shape parameter, t = the time in days, and τ = the mid height time at which half of the height at onset of reproduction had been reached. Curves were fitted to growth data of each family of each origin and at each site using family means based on 1-6 replicated plants. The growth rate (dy/dt) at mid height time was computed as in Frantzen (1994b):

$$v = b/(4*\tau).$$

The effects of origin and site on the parameters were analysed using two-way ANOVAs. The analyses were based on 1-5 family means per origin and site. As too few replicates per family survived until reproduction family effects were not analysed. Due to the resulting unbalanced design sequential sums of squares were calculated with origin as the biologically more interesting variable being entered into the model before site. Tukey`s test was used for multiple comparisons of means.

Analyses of variance, as described above, were used to determine the main effects of origin and site on time to emergence of seedlings, time to onset of reproduction, plant height at onset of reproduction, number of capitula and biomass. Biomass was log-transformed prior to analysis to meet the assumption of normality.

Analysis of habitat effects was also performed grouping data for logistic regression according to habitat and adding the contrast ruderal versus agricultural plants to the two-way ANOVAs.

Few plants rendered intact leaves for measurement of leaf area rust severity and therefore these data were not further analysed.

Table 4.1 Effects of origin and site on seedling emergence of three ruderal and three agricultural reciprocally transplanted *S. vulgaris* populations analysed by logistic regression. The origin by site interaction was included in the first run of the model but was in no case significant and was therefore removed from the model presented. The origin or site with the lowest emergence was chosen as reference for calculation of the odds ratio.

Effect	df	Wald-χ^2	P	Odds ratio (95% CI)[a]	Emergence[b]
Origin	5	20.92	0.008		
Ruderal					Average 58.0
Arconciel				2.08 (1.34-3.22)	62.8
Müntschemier				1.05 (0.68-1.61)	47.8
Courtepin				2.03 (1.31-3.14)	63.3
Agricultural					Average 53.3
Coussiberle				1.36 (0.89-2.10)	53.9
Corjolens				1.74 (1.13-2.68)	59.4
Praz				Reference	46.7
Site	5	70.69	< 0.001		
Ruderal					Average 50.4
Arconciel				4.36 (2.79-6.81)	64.4
Müntschemier				3.20 (2.06-4.96)	56.7
Courtepin				Reference	30.0
Agricultural					Average 60.9
Coussiberle				2.32 (1.50-3.59)	49.4
Corjolens				4.25 (2.72-6.64)	64.4
Praz				5.34 (3.40-8.41)	68.9

Fit of the model: $\chi^2 = 96.469$ df =10 P < 0.001

[a] An odds ratio > 1, i.e. 1 is not included in the 95% confidence interval, indicates a significantly increased probability of emergence compared to the reference.

[b] Emergence is expressed as percentage of seedlings emerging per origin or site.

Results

A significant habitat effect was only detected for the factor site, resulting in increased seedling establishment, survival, growth and reproduction as well as an increased rust incidence for plants at the agricultural sites compared to those at the ruderal sites (data not presented).

The total number of emerging seedlings was affected by origin of seeds as well as by site (Table 4.1). Seedlings from the origins Arconciel, Courtepin and Corjolens had an increased odd of emergence compared with seedlings from Praz. Compared to the site of Courtepin seedlings had a significantly higher probability to emerge at all other sites and seedlings originating from Courtepin showed maximum emergence at their home as well as at other ruderal sites (data not presented). Time to emergence showed strong environmental control, regardless of origin (data not presented).

The environment mainly determined survival of seedlings to onset of reproduction (Table 4.2). A significant origin by site interaction indicated that survival at the different sites was dependent on seed origin. However, the significance level for the interaction was

Table 4.2 Effects of origin and site on the survival of seedlings to onset of reproduction of three ruderal and three agricultural reciprocally transplanted *S. vulgaris* populations analysed by logistic regression. Origin was included in the first run of the model but was in no case significant and was therefore removed from the model presented. The origin or site with the lowest survival was chosen as reference for calculation of the odds ratio.

Effect	df	Wald-χ^2	P	Odds ratio (95% CI)[a]	Survival[b]
Site	5	12.41	0.030		
Ruderal					Average 28.6
Arconciel				1.69 (0.49-5.84)	39.7
Müntschemier				1.17 (0.32-4.30)	27.5
Courtepin				Reference	18.5
Agricultural					Average 57.4
Coussiberle				6.05(1.93-18.93)	64.0
Corjolens				2.75(0.97-7.83)	52.6
Praz				3.30(1.09-9.95)	55.6
Origin x site	25	38.10	0.045		

Fit of the model: χ^2 = 95.782 df = 30 P<0.001

[a] An odds ratio > 1, i.e. 1 is not included in the 95% confidence interval, indicates a significantly increased probability of emergence compared to the reference.

[b] Survival is expressed as percentage of seedlings surviving per origin or site.

marginal and got lost with individual removal of outliers.

Plant growth differed between seed origin as well as site. Examples of fitted growth curves with better or poorer fits are presented in Fig. 4.1. While the shape parameter *b* was

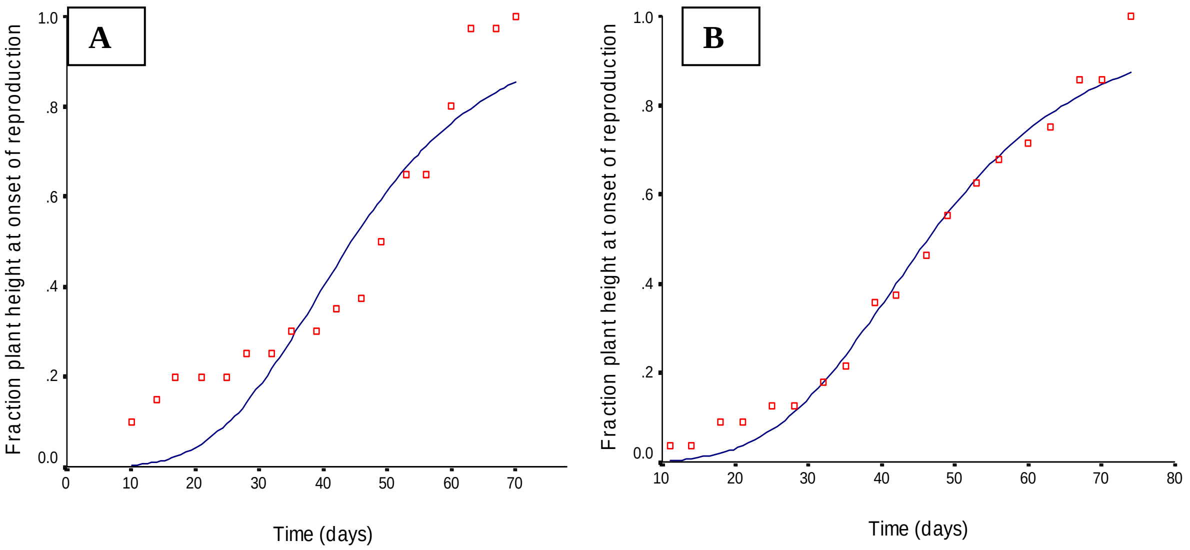

Fig 4.1 Examples of fitting curves to growth of *S. vulgaris* (see Table 4.4 for parameter estimates). **A** *S. vulgaris* originating from Arconciel grown at Arconciel and **B** *S. vulgaris* from Coussiberle grown at Corjolens.

Table 4.3 ANOVA of estimated parameters of a log-logistic model[a] fitted to growth data of three ruderal and three agricultural reciprocally transplanted *S. vulgaris* populations.

Parameter	Source	df	Mean Square	F value	P
b	Origin	5	0.550	2.144	0.067
	Site	5	6.441	25.110	< 0.001
	Origin x Site	24	0.187	0.730	0.809
	Error	98	0.257		
τ	Origin	5	83.875	4.877	0.001
	Site	5	202.452	11.772	< 0.001
	Origin x Site	24	19.551	1.137	0.320
	Error	98	17.197		
v	Origin	5	3.155E-05	2.724	0.024
	Site	5	2.763E-04	23.863	< 0.001
	Origin x Site	24	1.078E-05	0.931	0.561
	Error	98	1.158E-05		

[a] $y = 1/[1(1+\exp(-b*\ln(t/\tau)))]$, in which y = the fraction of plant height at onset of reproduction, b = a shape parameter, t = time in days, and τ = mid height time, at which $y = 0.5$. The growth rate v at mid height time was calculated as $b/(4*\tau)$.

only environmentally determined, the mid height time τ and the growth rate v were environmentally as well as genetically determined (Table 4.3). Plants originating from the ruderal site Courtepin took longer to reach the mid height time compared to other origins except those from the ruderal site Arconciel and plants from Arconciel had a significantly lower growth rate than those from the agricultural site Praz (Table 4.4). Fitted growth curves therefore resulted in slower growth for plants originating from Arconciel and Courtepin (Fig. 4.2A). Plants grown at the agricultural sites Coussiberle and Corjolens had the steepest shape parameters and the highest growth rates compared to the other sites (Table 4.4). Corjolens also had the shortest mid height time. These differences lead to faster growth at Coussiberle and Corjolens as shown in the fitted growth curves (Fig 4.2B).

All traits related to reproduction were determined by environmental as well as genetic variation (Table 4.5). Plants deriving from the agricultural origin Coussiberle had one of the shortest pre-reproductive periods, were the tallest at onset of reproduction, produced the maximum number capitula and the highest biomass at their home as well as at alien sites (Table 4.6). Plants originating from the ruderal populations Arconciel and Courtepin took longest to onset of reproduction and produced the lowest number of capitula. Plants growing at the agricultural sites of Coussiberle and Corjolens had the shortest pre-reproductive periods, the tallest plants at onset of reproduction, and the highest number of capitula and highest biomass. Plants at Courtepin had the longest pre-reproductive period and were the shortest plants at onset of reproduction producing the minimum number of capitula and lowest biomass.

Rust infection occurred at each site with rust incidence being solely influenced by the environment (Table 4.7). The lowest incidence was recorded at the ruderal site Courtepin and compared to this site the probability of infection at all other sites was significantly higher.

Table 4.4 Multiple comparisons (Tukey's Test) of estimated parameter means of a log-logistic model[a] fitted to growth data for three ruderal and three agricultural reciprocally transplanted *S. vulgaris* populations. Means with the same letter are not significantly different (95% confidence level). Means are based on 1 to 5 families with 1-6 replicated plants per family.

	Origin							
	Ruderal populations				Agricultural populations			
	Arconciel	Münt-schemier	Courtepin	Average	Coussiberle	Corjolens	Praz	Average
b	4.12a	4.38a	4.48a	4.33	4.43a	4.19a	4.49a	4.37
τ	48.6ab	46.3a	50.6b	48.5	46.4a	46.3a	45.7a	46.1
v	0.022a	0.024ab	0.023ab	0.023	0.024ab	0.023ab	0.025b	0.024

	Site							
	Ruderal populations				Agricultural populations			
	Arconciel	Münt-schemier	Courtepin	Average	Coussiberle	Corjolens	Praz	Average
b	3.76a	4.48b	3.98a	4.07	5.08c	4.61bc	3.87a	4.52
τ	47.4a	49.5a	49.9a	48.9	48.4a	42.1b	49.0a	46.5
v	0.020a	0.023a	0.020a	0.021	0.027b	0.028b	0.020a	0.025

[a] $y = 1/[1(1+\exp(-b*\ln(t/\tau)))]$, in which y = the fraction of plant height at onset of reproduction, *b* = a shape parameter, *t* = time in days, and τ = mid height time, at which $y = 0.5$. The growth rate *v* at mid height time was calculated as $b/(4*\tau)$.

Discussion

The present study demonstrated environmental as well as genetic variation of various life history traits related with plant fitness, being prerequisites for natural selection (Endler 1986). Survival was the only trait under exclusive environmental control. However, adaptation of *S. vulgaris* to its local environment could not be detected as indicated by the absence of significant origin by site interactions. Similar instances of non-adaptation were reported for *Agrostis capillaris* L. (Rapson and Wilson 1988) and *Bromus tectorum* (Rice and Mack 1991).

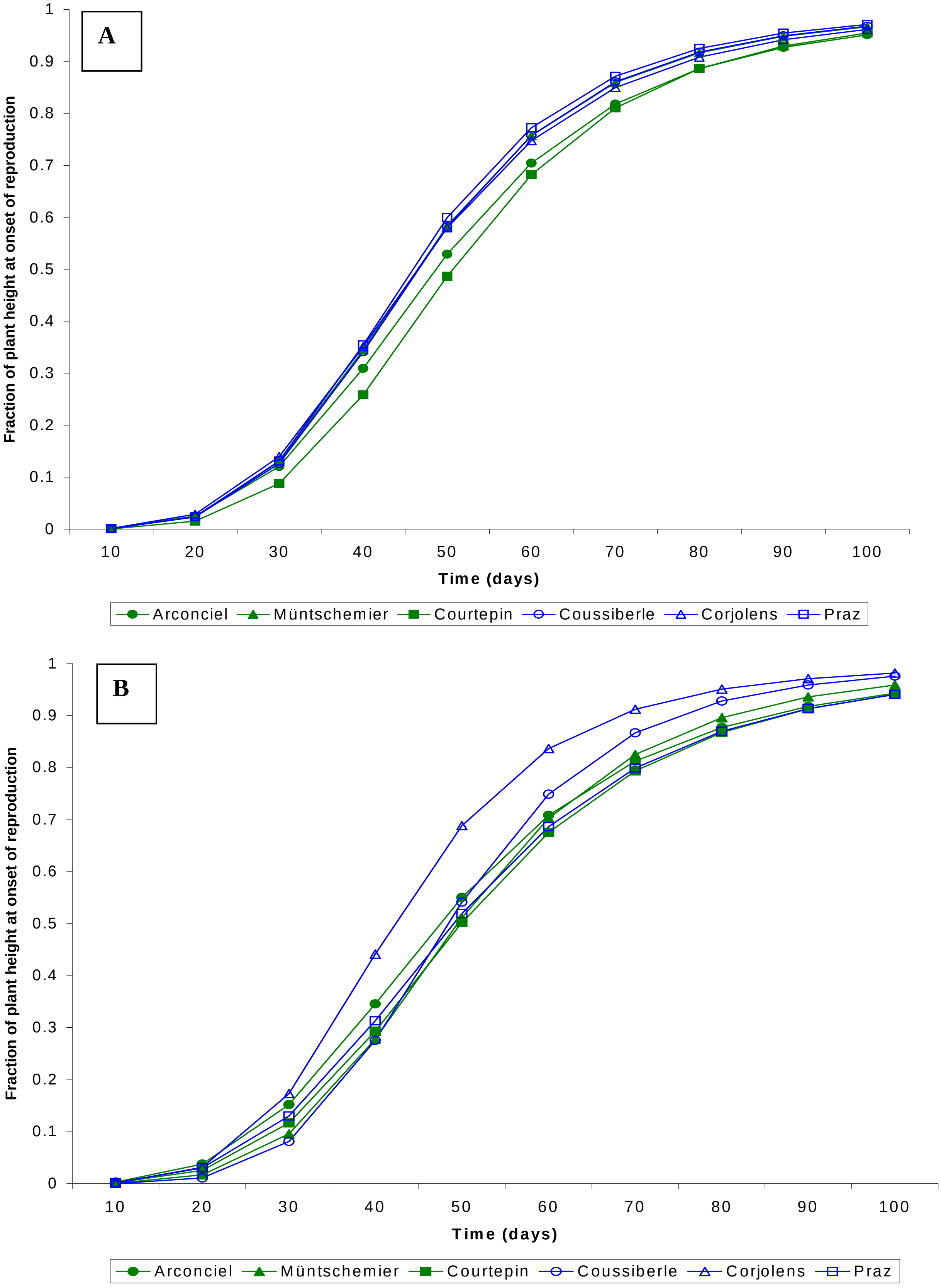

Fig. 4.2 Growth of *S. vulgaris* (see Table 4.4 for parameter estimates) relating to **A** origin and **B** site.

Table 4.5 ANOVA of vegetative and reproductive traits for three ruderal and three agricultural reciprocally transplanted *S. vulgaris* populations.

Trait	Source	df	Mean Square	F value	P
Time reprod. (days)	Origin	5	218.047	3.409	0.007
	Site	5	662.258	10.354	< 0.001
	Origin x Site	24	68.377	1.069	0.392
	Error	98	63.959		
Height reprod. (cm)	Origin	5	87.755	3.402	0.007
	Site	5	1051.673	40.770	< 0.001
	Origin x Site	24	13.383	0.519	0.966
	Error	98	25.795		
No. capitula	Origin	5	1139.489	2.977	0.015
	Site	5	20117.135	52.561	< 0.001
	Origin x Site	24	223.703	0.584	0.934
	Error	98	382.739		
Biomass[a] (g)	Origin	5	0.201	2.972	0.015
	Site	5	4.353	64.391	< 0.001
	Origin x Site	24	0.0314	0.464	0.983
	Error	98	0.0676		

[a] Data were log-transformed

Being an annual plant *S. vulgaris* has no other means than seed production for propagation emphasising the importance of the number of seedlings emerging with respect to fitness. Emergence of seedlings in general was higher at the agricultural sites probably providing more safe sites for germination. Germination in a safe site has been described as a stochastic event by Harper (1977) and studies of various perennials supported this view (McGraw and Antonovics 1983, Cheplick 1988, Rice and Mack 1991). In contrast genetic variation in the number of seedlings emerging was demonstrated for annual species (Cavers and Harper 1967, Van Groenendael 1985, Levin and Schmidt 1985). In the present study seeds originating from the ruderal site Courtepin showed maximum emergence at its home as well as at all other ruderal sites. However, no specific adaptation in the emergence of *S. vulgaris* was detected, which may be due to the uniform treatments of seeds at all sites facilitating germination by watering and eliminating competition.

There was no evidence of genetic variation resulting in differential survival of seedlings among *S. vulgaris* populations. This apparent lack of genetic differentiation in seedling survival has also been reported for other species (Antonovics and Primack 1982, Van Groenendael 1985, Levin and Schmidt 1985, Cheplick 1988, Rice and Mack 1991, Van Tienderen and Van der Toorn 1991). The importance of unpredictable stochastic environmental factors affecting seedlings, causing their survival to be more dependent on the absence of unfavourable conditions than on its own particular genotype, has been emphasised by Antonovics and Primack (1982). Conversely, genetic differences in seedling survival have been noted by McGraw and Antonovics (1983) and Schmidt and Levin (1985). The probability of seedling survival in the present study was generally increased at all agricultural sites, which suggests that conditions are more favourable in this habitat, possibly due to

Table 4.6 Multiple comparisons of vegetative and reproductive trait means (Tukey's Test) for three ruderal and three agricultural reciprocally transplanted *S. vulgaris* populations. Means with the same letter are not significantly different (95% confidence level). Means are based on 1 to 5 families with 1-6 replicated plants per family.

	Origin							
	Ruderal populations				Agricultural populations			
	Arconciel	Müntschemier	Courtepin	Average	Coussiberle	Corjolens	Praz	Average
Time reprod. (d)	83.8b	76.2a	80.6ab	80.2	76.0a	78.7ab	75.8a	76.8
Height reprod. (cm)	21.5ab	22.6ab	21.6ab	21.9	25.1b	19.5a	23.3ab	22.6
No. capitula	37.2ab	37.7ab	28.7a	34.5	48.1b	44.8ab	36.3ab	43.1
Biomass (g)[a]	3.75ab	2.19a	2.71ab	2.88	4.09b	2.56ab	2.86ab	3.17

	Site							
	Ruderal populations				Agricultural populations			
	Arconciel	Müntschemier	Courtepin	Average	Coussiberle	Corjolens	Praz	Average
Time reprod.(d)	83.8c	79.2bc	84.3c	82.4	74.6ab	71.2a	83.3c	76.4
Height reprod.(cm)	15.7a	15.4a	12.6a	14.6	27.3bc	23.9b	30.6c	27.2
No. capitula	12.3a	21.3a	10.4a	14.7	77.8b	67.4b	19.9a	55.0
Biomass (g)[a]	0.82ab	1.15bc	0.46a	0.81	8.53d	3.56e	1.51c	4.53

[a] Data were log-transformed. Untransformed means are presented

improved soil structure and nutrient status.

Infection by *P. lagenophorae* was not an important mortality factor for *S. vulgaris*. Rust infection occurred at all sites with the number of infected plants being solely dependent on the environment. Sites with maximum plant mortality did not correspond with the sites of

Table 4.7 Effects of origin and site on rust incidence of three ruderal and three agricultural reciprocally transplanted *S. vulgaris* populations analysed by logistic regression. Origin was included in the first run of the model but was in no case significant and was therefore removed from the model presented. The site with the lowest incidence was chosen as reference for calculation of the odds ratio.

Effect	df	Wald-χ^2	P	Odds ratio (95% CI)[a]	Incidence[b]
Site	5	58.61	< 0.001		
Ruderal					Average 31.9
Arconciel				34.75 (8.08-149.48)	58.8
Müntschemier				12.01 (2.76-52.20)	33.0
Courtepin				Reference	3.8
Agricultural					Average 52.9
Coussiberle				26.16 (5.99-114.15)	52.8
Corjolens				58.19 (13.36-253.47)	69.6
Praz				14.43 (3.36-62.02)	36.3

Fit of the model: χ^2 = 91.942 df = 5 P<0.001

[a] An ratio > 1, i.e. 1 is not included in the 95% confidence interval, indicates a significantly increased probability of emergence compared to the reference.

[b] Incidence is expressed as percentage of plants infected per origin or site.

maximum rust incidence. It seems that fungal spores for infection are widely distributed but that infection depends upon favourable conditions for spore germination. In general rust incidence was higher at the agricultural sites compared to the ruderal ones. At the sites of Coussiberle and Corjolens irrigation might have improved distribution and germination of spores, while plants at the site of Praz were shaded by the vine, possibly improving conditions for spore germination. Nevertheless, the increased rust incidence at the agricultural sites did not result in a higher disease impact on plant growth and reproduction, indicating that *P. lagenophorae* is not a major selection factor in populations of *S. vulgaris*. Plants deriving from different origins were all susceptible to rust infection. However, disease severity, which in this experiment could not be determined, might have differed between plants from different origins as race-nonspecific quantitative resistance of *S. vulgaris* to infection by *P. lagenophorae* as has been reported by Wyss and Müller-Schärer (1999).

Differences in growth rate of *S. vulgaris* were apparent among origins as well as sites. Plants originating from the ruderal sites Arconciel and Courtepin grew slower than plants of all other origins. Both derived from sites characterised by relatively unfavourable soil conditions with Arconciel being a stony gravelpit and Courtepin a waste ground with a very shallow and strongly compacted soil surface. Although growth was reduced, resulting in a relatively long pre-reproductive period and smaller plant size, both plant origins reached reproduction even if the number of produced capitula was low compared to other origins. These findings suggest that *S. vulgaris* is able to endure unfavourable environments reducing both vegetative and reproductive vigour following the strategy of a stress tolerator (Grime 1979). Conversely, plants originating from the agricultural site Coussiberle grew fastest and had the highest reproduction at the home as well as at alien sites. Regarding site effects, plants at the agricultural sites Coussiberle and Corjolens generally grew faster than at all other sites and had the highest reproduction. These sites are characterised by relatively favourable soil conditions including soil nutrients. In addition, Corjolens was irrigated regularly during

August, while Coussiberle was watered occasionally. In such an environment *S. vulgaris* seems to behave like an r-strategist (Grime 1979) being able to exploit a productive environment for rapid plant growth maximising seed production. Such a strategy is of advantage at sites with a relatively high level of disturbance like at agricultural sites with their cultivation practices. Although disturbance was not included in the present study, high reproduction at the agricultural sites Coussiberle and Corjolens may indicate adaptation to disturbance possibly linked with the greater productivity of these sites based on factors like higher nutrient levels. Early and high reproduction as local adaptation of *Stellaria media* to the disturbance of agricultural habitats has been demonstrated by Sobey (1987). Briggs and Block (1992) reported shorter pre-reproductive periods for *S. vulgaris* as an adaptation to intensive weeding.

Although specific adaptation of the various life history traits studied was not detected, results of the present study indicate the potential of *S. vulgaris* to adapt to its environment, which makes it unlikely that genetic differentiation of *S. vulgaris* has resulted from other evolutionary forces than natural selection. Emergence, growth and fecundity showed genetic as well as environmental variation. Survival of *S. vulgaris*, determined only by the environment, depended not on infection by *P. lagenophorae* but on other, stochastic, mortality factors. With all other life history traits supporting the prerequisites of natural selection it is likely that random environmental events occurring during the experiment obscured the presence of local adaptation and that in the absence of stochastic mortality *S. vulgaris* has the potential to adapt to its environment.

Acknowledgements

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5

General discussion and Outlook

The system management approach of biological control is aimed at managing a weed pathosystem in such a way to stimulate disease epidemics on the target weed population and reducing the competition exerted by the weed on a crop (Frantzen and Müller-Schärer 1998). This can be achieved by i) introduction of a relatively small amount of inoculum in a weed population at an appropriate time ii) careful selection and manipulation of the genetic composition of the pathogen population and iii) specific management of infection conditions (Müller-Schärer and Frantzen 1996). The system management approach is developed using the weed pathosystem *S. vulgaris – P. lagenophorae*. In the following the results of the present thesis will be discussed with respect to this pathosystem regarding the biological control of *S. vulgaris* in general and the use of the three strategies of the system management approach in particular.

Substantial differences were observed in the population dynamics of *S. vulgaris* at ruderal and agricultural habitats (Chapter 2). Plants of *S. vulgaris* at the ruderal habitat survived over winter, resulting in greater population sizes and a majority of plants in flower and seed set in spring. At the agricultural, habitat where *S. vulgaris* is inhibited to winter due to weed control measures in autumn or early spring, population sizes in spring were smaller with mainly vegetative plants. The observed difference in the population dynamics of *S. vulgaris* resulted in divergent dynamics of *P. lagenophorae* in ruderal and agricultural habitats. At the ruderal habitat the rust occurred already in spring implying that *P. lagenophorae* survived as mycelium within the host during winter as it has been demonstrated by Frantzen and Müller-Schärer (1999). At the agricultural habitat no rust infection occurred before summer as a result of the limited number of suitable hosts in spring (Chapter 2). 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. In both habitats mature plant stages were more susceptible to rust infection compared to vegetative plant stages. Increased rust severity at older plant stages (4th leaf stage) compared to younger ones (2nd leaf stage) has also been demonstrated in experiments under controlled conditions (Wyss and Müller-Schärer 1999).

Rust incidence in both habitats was highest in autumn. A higher rust incidence in autumn than in spring has also been observed by Paul and Ayres (1986a) in field experiments. Results indicate that survival of host and pathogen during winter is critical to the start of an epidemic of *P. lagenophorae* in a *S. vulgaris* population. It therefore seems a feasible strategy to adapt weed control regimes in order to allow *S. vulgaris* plants to winter. Infected plants, surviving winter, may serve as inoculum sources to induce new rust epidemics in spring, and non-infected plants provide mature plant stages, being more susceptible to rust infection enhancing rust epidemics.

Survival of field grown *S. vulgaris* over winter however, is reduced by *P. lagenophorae* infection (Paul and Ayres 1986a, Frantzen and Müller Schärer 1999). Measurements of the survival of infected *S. vulgaris* over winter at two agricultural sites, a vineyard and an apple orchard, were conducted in the framework of this thesis (data not presented). Mortality of *S. vulgaris* was 99% and 82% respectively with no differences between plants bearing aecidia of the rust in autumn and those without, demonstrating a general high mortality of *S. vulgaris* over winter. Frantzen and Müller-Schärer (1999) also observed 93% mortality of *S. vulgaris* over winter without a significant difference between plants with and without aecidia in autumn. The results of the present thesis and the studies of Paul and Ayres (1986a) and Frantzen and Müller-Schärer (1999) point at relatively low amounts of inoculum in *S. vulgaris* populations in spring delaying epidemics of *P. lagenophorae*. This suggests that an increase of the amount of inoculum may enhance epidemics in spring. This might be achieved by wintering of infected *S. vulgaris* in environmentally favourable areas or in protected tunnels and greenhouses from where infected plants can be introduced into *S. vulgaris* populations as inoculum sources. In short-lived annual crops, such as vegetables, which alternate throughout the growing season, new introductions of inoculum are necessary. Once an epidemic is started in spring, a reservoir of rust infected *S. vulgaris,* like for example in field margins or green cover strips, should therefore be maintained as inoculum sources. The number of infected *S. vulgaris* plants needed to start an epidemic and their spacing in the crop to achieve uniform spread of the disease is currently under investigation. Furthermore the timing of inoculum introduction is subject of current research to provide sufficient infection in *S. vulgaris* populations during the critical period of the crop, in which it is most susceptible to competition by the weed. Both aspects are studied under field conditions in co-operation with farmers. Incorporating wintering of *S. vulgaris* to provide more inoculum sources would be an important extension of these ongoing field trials.

The population dynamics of *S. vulgaris* and *P. lagenophorae* were analysed with respect to short-term consequences of biological control (Chapter 2). Long-term consequences have not been investigated so far. It therefore would be interesting to incorporate the demographic data collected in the present thesis into a population matrix model. Field data on seed output and subsequent germination have to be collected to run such a model. If so, predictions about changes in population size on the long-term are possible. In this context it would be of special interest to conduct a sensitivity analysis adding infection of plants with *P. lagenophorae* to the model. In this way the development stage of *S. vulgaris* most sensitive to infection could be identified and changes in the population dynamics of *S. vulgaris* due to infection by *P. lagenophorae* could be predicted.

As a continuation of the demographic study (Chapter 2) molecular studies using AFLP-markers will be conducted. This technique allows to determine temporal changes in the genetic composition of populations. At the agricultural habitat the spring generation as well as subsequent generations seem to build-up by re-colonisation due to weed control measures. This implies that the genotype composition of agricultural populations may very from year to year as well as within a year. In contrast, at the ruderal habitat populations are mainly built-up by wintering plants producing seeds in spring, which subsequently germinate establishing next generations. The genotype composition of these populations is expected to be relatively stable.

Plants of *S. vulgaris* from ruderal and agricultural habitats were genetically different in their response to additional nutrients, suggesting nutrient specific genetic differentiation. Genetic differentiation of *S. vulgaris* with respect to infection by *P. lagenophorae* could not be detected (Chapter 3). Rust infection significantly decreased vegetative biomass and reproductive output without significant differences in the response to infection between plant families. In contrast, Wyss and Müller-Schärer (1999) studying various *S. vulgaris* and *P. lagenophorae* lines reported a continuos range of variation in susceptibility of the plant lines. No differential genetic interactions, indicating race-nonspecific quantitative resistance, were detected in this study. They defined disease severity as leaf tissue of the first or second true leaf occupied by mycelium and this parameter may not be related to reproductive output. Differences in disease severity early in the plant development might be compensated for while further growing and might therefore not be expressed in reproductive characters. The absence of detectable genetic variation in fitness parameters of *S. vulgaris* plants to infection by *P. lagenophorae* may hinder the build-up of resistant weed populations and sustainability of biological weed control might be achieved. Successful infection of different plant families with one rust line also suggests the potential of using a single rust line as a biological control agent. Another factor to be considered in this context is the genetic variability of *P. lagenophorae* possibly leading to differences in disease severity. Wyss and Müller-Schärer (1999) indicated differences in the aggressiveness of rust lines. However, genetic variation of the rust might be limited since it seems that only the asexual cycle of the fungus is completed. The genetic variation of rust populations is currently investigated. With the study of the genetic variation of *P. lagenophorae* being currently under way it would be interesting to determine whether the rust occurring at the different ruderal and agricultural sites is genetically uniform or whether different rust lines occur at different sites. If so, studies of host-pathogen interactions, conducted with the different *S. vulgaris* and *P. lagenophorae* lines would be an important extension of the investigation on resistance. Measuring disease severity as leaf tissue occupied by mycelium as well as a parameter related to reproductive output, would allow to asses whether differences in disease severity early in plant development are also expressed in reproductive characters. If so, the leaf tissue of the first and second true leave occupied by mycelium could be used as a general predictor for disease severity.

The reproductive output of *S. vulgaris* was substantially reduced through infection by *P. lagenophorae*. (Chapter 3). However, absence of detectable genetic variation in fitness parameters of *S. vulgaris* plants to infection by the rust suggests that *P. lagenophorae* is not an important selection factor in *S. vulgaris* populations at present. This result was confirmed by the transplant experiment demonstrating that an increased rust incidence at the agricultural sites did not result in a higher disease impact on plant growth and reproduction (Chapter 4). Furthermore, an increased disease incidence could not be related to a reduction in plant numbers (Chapter 2) and rust infection did not specifically affect the survival of *S. vulgaris* (Chapter 4), indicating that *P. lagenophorae* is not a major mortality factor in *S. vulgaris* populations. In contrast Paul and Ayres (1986a) reported substantial mortality of field grown *S. vulgaris* infected with rust in autumn and spring. Mortality in autumn mainly occurred at the seedling stage due to hypocotyl infection by secondary pathogens, while mortality in spring was caused by reduced survival of infected plants over winter. Seeds for the transplant experiment were sown end of summer with most of the seedlings emerging in August and September. Rust incidence at this stage was very low probably due the mainly vegetative plants. Furthermore, the warm and dry conditions of this time of the year might have inhibited secondary pathogens, which are usually favoured by the cool, damp conditions of autumn. Later during the experiment, when these conditions were met, plants were already further developed, showing a higher rust incidence but possibly being less susceptible to infection by secondary pathogens. Thus the potential of the rust to kill *S. vulgaris*, provided suitable development stages of the host are present, may be limited to autumn and subsequent adverse winter conditions as suggested by Frantzen and Hatcher (1997). The rust *P. lagenophorae* may thus be a potential mortality factor in *S. vulgaris* populations depending on the season. Differential mortality of *S. vulgaris* due to rust infection could then lead to natural selection. However, differential mortality of rust infected *S. vulgaris* over winter could neither be observed in this thesis (data not presented) nor in other studies (Frantzen and Müller-Schärer 1999). In the transplant experiment rust infection occurred at all sites with plants from different origins appearing equally susceptible to rust infection (Chapter 4). Nevertheless, rust severity, which in this experiment could not be determined, might have differed between plants from different origins. However, in view of the results of the greenhouse experiment demonstrating uniform responses to rust infection of *S. vulgaris* of different origins (Chapter 3), this seems unlikely. Results of this thesis indicate that at present *P. lagenophorae* is not an important selection factor in *S. vulgaris* populations altering their genetic composition possibly resulting in resistant genotypes. On the long-term however, especially in view of an increased disease pressure due to biological control, *P. lagenophorae* might be a selection factor in populations of *S. vulgaris.* To further resolve the role of *P. lagenphorae* as a selection factor, selection coefficients could be determined, based on broad sense heritabilities, defined as the ratio of genetic variance to phenotypic variance. Although the amount of genetic and phenotypic variance could be estimated using the data used of this thesis, accurate estimation of broad sense heritabilities needs to be based on at least fifteen plant families compared to the five used in this thesis. Alternatively, a more accurate but long term study would be artificial selection experiments, comprising several generations in which the change in gene frequency of parents and offspring caused by rust infection could be determined.

Populations of *S. vulgaris* at the agricultural habitat exhibited high genetic variation in comparison to ruderal populations (Chapter 3). Nevertheless the different agricultural families showed the same response to rust infection causing substantial reductions in vegetative biomass and reproductive output. It has been assumed that populations of less genetic variation may be more easily controlled by biological control (Barrett 1982). However, results presented here demonstrate the potential of biological control in populations of greater genetic variability. As stated by Barrett (1982) the nature of genetic variation present in a population and how this will influence plant responses may be more important than the amount of genetic variation.

Rust infection occurred at all sites, being dependent on availability and developmental stage of the host as well as environmental conditions (Chapter 2, Chapter 4). It seems that fungal spores for infection are widely distributed and that, in the presence of suitable hosts, infection depends on favourable conditions for spore germination such as sufficient humidity. Irrigation at the time of inoculum introduction might improve distribution and germination of spores, enhancing rust incidence. Plants of *S. vulgaris* with additional nutrient applications showed a stronger response to infection by *P. lagenophorae* (Chapter 3). Paul and Ayres (1986c) also reported an enhanced negative impact of the rust on well nourished plants. The agricultural sites investigated were characterised by a higher amount of soil nutrients due to fertilisation (data not presented). To maximise the susceptibility of the host timing of fertiliser applications might be adjusted to coincide with inoculum introduction as suggested by Paul *et al.* (1990). To implement irrigation and fertilisation to enhance biological control, such a strategy has to undergo field trials and needs to be tested in practical agriculture in co-operation with farmers.

The results of the present thesis support the biological control of *S. vulgaris* with *P. lagenophorae* using the system management approach. Management of the pathosystem to stimulate rust epidemics can be achieved by i) wintering and maintaining reservoirs of infected *S. vulgaris* plants as inoculum sources ii) a single rust line serving as inoculum and iii) improvement of infection conditions through irrigation and fertilisation at the time of inoculum introduction.

Summary

Phenotypic plasticity and genetic differentiation of the annual weed *Senecio vulgaris* L. from ruderal and agricultural habitats were investigated to evaluate the implications for its biological control with the rust fungus *Puccinia lagenophorae* Cooke using the system management approach.

Weed demographic studies are a prerequisite to any weed control strategy. The population dynamics of *S. vulgaris* and *P. lagenophorae* at ruderal and agricultural habitats was investigated (Chapter 2). Seedling establishment appeared to be a major factor influencing *S. vulgaris* population dynamics. The importance of seedling establishment, together with the observed short generation time of 5 weeks and the broad range of plant sizes at reproduction classified *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 and a majority of plants in flower and seed set in spring. At the agricultural habitat, where only a few *S. vulgaris* winter due to weed control measures, population sizes in spring were smaller with mainly vegetative plants. The observed difference in the population dynamics of *S. vulgaris* resulted in divergent dynamics of *P. lagenophorae* in ruderal and agricultural habitats. At the ruderal habitat the rust occurred already in April, while at the agricultural habitat it did not appear before August. This suggests that the rust survives over winter as mycelium within the host at the ruderal habitat, whereas it could not survive over winter at the agricultural habitat due the relatively low number of wintering hosts. 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. 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.* Survival of *S. vulgaris* over winter provides inoculum sources inducing new rust epidemics in spring with mature plant stages being more susceptible to infection, enhancing rust epidemics.

Phenotypic plasticity and genetic differentiation of *S. vulgaris* from ruderal and agricultural habitats were assessed in a greenhouse experiment (Chapter 3). Vegetative and reproductive responses of ruderal and agricultural plants grown at two nutrient levels (high/low) and two rust environments (presence/absence) were compared. Plants of *S. vulgaris* from ruderal and agricultural habitats were genetically different with agricultural plants having a larger leaf area and a higher reproductive output. They also showed a stronger plastic response of reproductive traits to nutrients. Results suggest that genetic differentiation among habitats is nutrient specific. An increased reproductive output might me of advantage in the agricultural habitat with its disturbance due to cultivation practices. Due to the minor importance of the soil seed bank, populations have to re-establish through re-colonisation. An increased reproductive output improves seed dispersal enabling *S. vulgaris* to quickly re-establish new patches at favourable sites. Genetically different families of *S. vulgaris* were only detected at the agricultural habitat. Plasticity of reproductive characters in response to nutrients was also genetically different among agricultural families. Genetic differentiation of *S. vulgaris* due to infection by *P. lagenophorae* could not be observed. Plants with additional nutrient application showed a stronger response to rust infection. Rust infection significantly decreased vegetative biomass and reproductive output with no differences in the response to infection between plant families, suggesting that *P. lagenophorae* is not an important

selection factor in *S. vulgaris* populations at present. Successful infection of different plant families with one rust line also suggests the potential of using a single rust line as a biological control agent.

A reciprocal seed transplant experiment was conducted to determine environmental and genetic variation of life history traits in *S. vulgaris* from ruderal and agricultural habitats in the field and their potential for local adaptation through natural selection (Chapter 4). Emergence, growth and fecundity showed environmental as well as genetic variation. However, there was no indication of local adaptation. Seedling survival was solely under environmental control stressing the importance of stochastic events for plant mortality. Plants originating from ruderal sites mainly performed like stress tolerators showing reduced growth, but nevertheless reaching reproduction. Plants at most agricultural sites behaved like r-strategists exploiting a productive environment for rapid plant growth maximising seed production. Emergence, survival growth and fecundity were higher at the agricultural sites compared to the ruderal ones. Infection by *P. lagenophorae* occurred at all sites, with the highest incidence at the agricultural sites, and was solely dependent on the environment. It seems that fungal spores for infection are widely distributed and that, in the presence of suitable hosts, infection depends on favourable conditions for spore germination. A higher incidence did not result in an increased disease impact nor did it specifically affect the survival of *S. vulgaris*, suggesting that *P. lagenophorae* is not a major mortality factor in populations of *S. vulgaris*. With all other life history traits supporting the prerequisites of natural selection it is likely that in the absence of stochastic mortality *S. vulgaris* has the potential to adapt to its environment.

The results of the present thesis are summarised and discussed with respect to biological control of *S. vulgaris* in general and the use of the system management approach in particular and subsequent studies based on the results of the present thesis are proposed (Chapter 5). In the absence of detectable genetic variation of *S. vulgaris* plants to infection by *P. lagenophorae* and the minor importance of the rust as a selection factor in *S. vulgaris* populations at present, the potential of the system management approach for the biological control of *S. vulgaris* is supported by the results of the present thesis. Management of the pathosystem to stimulate rust epidemics can be achieved by i) wintering of *S. vulgaris* plants as inoculum sources ii) single rust lines serving as inoculum and iii) improvement of infection conditions through irrigation and fertilisation at the time of inoculum introduction.

Zusammenfassung

Phenotypische Plastizität und genetische Differenzierung des annuellen Unkrautes *Senecio vulgaris* L. aus ruderalen und landwirtschaftlichen Habitaten und ihre Relevanz in Bezug auf die biologische Kontrolle mit dem Rostpilz *Puccina lagenophorae* Cooke, unter Anwendung des `System Management Approach`, waren Gegenstand dieser Dissertation.

Demographische Studien der Unkrautpopulation sind eine Voraussetzung für jegliche Unkrautbekämpfungsmaβnahme. Daher wurde die Populationsdynamik von *S. vulgaris* und *P. lagenophorae* aus ruderalen und landwirtschaftlichen Habitaten untersucht (Kapitel 2). Die Etablierung von Keimlingen scheint ein wichtiger Einflussfaktor auf 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 Pflanzengröβe 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 gröβere Population sowie eine Mehrzahl an blühenden und Samen bildenden Pflanzen im Frühjahr zur Folge hatte. Im landwirtschafltichen Habitat konnte *S. vulgaris* aufgrund von Unkrautkontrollmaβnahmen kaum überwintern, sodaβ die Populationen im Frühjahr kleiner waren mit der Mehrzahl der Pflanzen im vegetativen Stadium. Der Unterschied in der Populationsdynamik von *S. vulgaris* zwischen den Habitaten bedingte eine unterschiedliche Dynamik von *P. lagenophorae* aus ruderalen und landwirtschaftlichen Habitaten. Im ruderalen Habitat trat der Rost bereits im April auf, während er im landwirtschaftlichen Habitat nicht vor August anzutreffen war. Dies weist daraufhin, daβ der Rost im ruderalen Habitat als Myzel innerhalb der Wirtspflanze überwintert, während er im landwirtschaftlichen Habitat aufgrund mangelnder Wirtspflanzen nicht überwintern kann. Rost Epidemien im landwirtschaftlichen Habitat im Frühjahr scheinen nicht nur durch die geringe Menge an Inokulum verhindert zu werden, sondern auch durch die Mehrzahl an Pflanzen in jungen Entwicklungsstadien verglichen mit dem ruderalen Habitat. In beiden Habitaten waren reproduktive Pflanzenstadien anfälliger für eine Infektion mit dem Rost als vegetative Stadien. Die Manipulation der Wirtspflanzendynamik über Winter zur Förderung von Rost Epidemien könnte als biologische Kontollmaβnahme eingesetzt werden. Überwinternde *S. vulgaris* Pflanzen dienen als Inokulum Quellen im Frühjahr von denen Rost Epidemien ausgehen und stellen reifere und somit für den Rost anfälligere Entwicklungsstadien, was die Entwicklung von Rost Epidemien fördert.

Phenotypische Plastizität und genetische Differenzierung von *S. vulgaris* aus ruderalen und landwirtschaftlichen Habitaten wurden in einem Gewächshaus Experiment bestimmt (Kapitel 3). Vegetative und reproduktive Merkmale von ruderalen und landwirtschaftlichen Pflanzen, die unter hohem oder niedrigem Nährstoffangebot und mit oder ohne Infektion mit *P. lagenophorae* angezogen waren, wurden verglichen. Pflanzen von *S. vulgaris* aus ruderalen und landwirtschaftlichen Habitaten waren genetisch unterschiedlich. Die landwirtschaftlichen Pflanzen zeichneten sich durch eine gröβere Blattfäche sowie eine höhere Reproduktion aus. Sie wiesen auch eine plastischere Reaktion der reproduktiven Merkmale auf ein höheres Nährstoffangebot auf. Diese Ergebnisse weisen daraufhin, daβ die genetische Differenzierung zwischen den Habitaten auf Unterschiede im Nährstoffangebot beruht. Im landwirtschaftlichen Habitat, bedingt durch Kultivierungsmaβnahmen, welche die Populationen von *S. vulgaris* störend beeinfluβen, könnte eine erhöhte Reproduktion von

Vorteil sein. Die Samenbank ist für *S. vulgaris* von geringer Bedeutung und daher müssen sich die Populationen durch Re-Kolonisierung erneut etablieren. Eine erhöhte Reproduktion erhöht auch die Samenverbreitung, sodaβ *S. vulgaris* in der Lage ist sich rasch an dafür geeigneten Stellen neu zu etablieren. Genetisch unterschiedliche Familien von *S. vulgaris* wurden nur im landwirtschaftlichen Habitat gefunden. Die landwirtschaftlichen Familien unterschieden sich auch in Bezug auf die Plastizität von reproduktiven Merkmalen auf ein höheres Nährstoffangebot. Eine genetische Differenzierung von *S. vulgaris* auf Grund von Infektion mit *P. lagenophorae* konnte nicht gefunden werden. Pflanzen mit einem höherem Nährstoffangebot zeigten eine stärkere Reaktion auf die Infektion mit dem Rost. Infektion mit dem Rost hatte eine signifikante Verringerung der Blattfläche, der vegetativen Biomasse sowie der Reproduktion zur Folge, ohne Unterschiede der Reaktionen auf Infektion zwischen den unterschiedlichen ruderalen und landwirtschaftlichen Familien. Dies weist daraufhin, daβ *P. lagenophoarae* gegenwärtig als Selektionsfaktor für *S. vulgaris* Populationen von untergeordneter Bedeutung ist. Weiterhin zeigt die erfolgreiche Inokulation verschiedener Pflanzenfamilien mit einer Rostlinie das Potential einzelner Rostlininen als biologische Kontrollorganismen an.

Die umweltbedingte und genetische Variation von lebensgeschichtlichen Merkmalen von *S. vulgaris* aus ruderalen und landwirtschaftlichen Habitaten im Feld und deren Potential zur lokalen Adaptation durch natürliche Selektion wurde in einem reziproken Samen Transplantations Experiment untersucht (Kapitel 4). Keimung, Wachstum und Fertilität wurden durch umweltbedingte als auch genetische Variation bestimmt. Jedoch konnten keine Hinweise auf lokale Adaptation gefunden werden. Das Überleben von Keimlingen bis zur Samenproduktion wurde allein durch Umwelteinflüβe bedingt, was die Bedeutung von stochastischen Faktoren für die Mortalität von Pflanzen hervorhebt. Pflanzen, die aus den ruderalen Standorten stammten, wiesen ein reduzierten Wachstum auf, produzierten jedoch Samen, und verhielten sich somit wie stress-tolerante Pflanzen. Pflanzen, die in den landwirtschaftlichen Standorten wuchsen, zeigten das Verhalten von r-Strategen, welche eine produktive Umwelt für ein rasches Wachstum und eine maximale Produktion von Samen nutzen. Etablierung von Keimlingen, Überleben, Wachstum und Fertilität waren in den landwirtschaftlichen Standorten im Vergleich zu den ruderalen erhöht. Infektion mit *P. lagenophorae* trat in allen Standorten auf, mit der höchsten Infektionsrate in den landwirtschaftlichen Standorten, und war rein von der Umwelt abhänging. Es scheint, daβ Pilzsporen für eine Infektion weit verbreitet sind und in Anwesenheit geeigneter Wirte, die Infektion von günstigen Umweltbedingungen für die Sporenkeimun abhängig ist. Eine höhere Infektionsrate wirkte sich jedoch nicht in einem erhöhten Krankheitsdruck auf Pflanzenwachstum-und reproduktion aus, noch wurde das Überleben von *S. vulgaris* Pflanzen durch Infektion mit dem Rost beeinfluβt, was daraufhin weist, daβ *P. lagenophorae* kein wichtiger Mortalitätsfaktor für Populationen von *S. vulgaris* ist. Alle anderen lebensgeschichtlichen Merkmale wiesen die Voraussetzungen für natürliche Selektion auf. Daher ist anzunehmen, daβ sich *S. vulgaris*, in der Abwesenheit von stochastischen Mortalitätsfaktoren, potentiell an seine lokale Umgebung anpassen kann.

Abschlieβend wurden die Resultate dieser Dissertation zusammengefaβt und in Bezug auf die biologische Kontrolle von *S. vulgaris* im allgemeinen und die Anwendung des ‘System Management Approach` im speziellen diskutiert, sowie mögliche Folgestudien, die auf Ergebnissen dieser Dissertation beruhen, vorgestellt. (Kapitel 5). Da keine genetische Variation von *S. vulgaris* Pflanzen in Bezug auf Infektion mit *P. lagenophoarae* nachgewiesen werden konnte und der Rost gegenwärtig als Selektionsfaktor für *S. vulgaris* Populationen von untergeordneter Bedeutung ist, unterstreichen die Ergebnisse dieser

Dissertation das Potential des `System Mangement Approach` für die biologische Kontrolle von *S. vulgaris*. Diese Methode ist darauf ausgerichtet Epidemien von *P. lagenophorae* auf *S. vulgaris* zu stimulieren, was durch folgende Maβnahmen erreicht werden kann: i) die Überwinterung von infizierten *S. vulgaris* Pflanzen als Inokulum Quellen, ii) die Verwendung einzelner Rostlinien als Inokulum und iii) die Optimierung von Infektionsbedingungen durch Bewässerung und Düngung zum Zeitpunkt der Ausbringung von Inokulum.

Résumé

La plasticité phénotypique et la différentiation génétique de la mauvaise herbe annuelle *Senecio vulgaris* L. dans le habitats rudéraux et agricoles ont été étudiées afin d`évaluer les implications pour son contrôle biologique avec la rouille *Puccinia lagenphorae* Cooke en utilisant l`approche dite “system management”.

Les études démographiques des mauvaises herbes sont une nécessité pour toute stratégie de contrôle des mauvaises herbes. Pour cela, la dynamique des populations de *S. vulgaris* et *P. lagenphorae* se trouvant dans des habitats rudéraux et agricoles a été examinée (chapitre 2). L`établissement de plantes germinales semble être un facteur important influençant la dynamique des populations de *S. vulgaris*. Cette derniére peut être qualifiée de stratége rudéral sur la base de l`importance de l`établissement de plantes germinales, sur l`observation que cing semaines sont nécessaires pour une génération ainsi que sur le large spectre de taille des plantes se trouvant à l`état reproductif. Il a été observé que la dynamique des populations est différente entre les habitats rudéraux et agricoles. Les plantes de l`habitat rudéral hivernent, donc, au printemps les populations sont plus importantes, avec une majorité des plantes en fleurs et produisant des semences. Par contre, dans l`habitat agricole, *S. vulgaris* n`hiverne quasiment pas, ceci a cause des mesures de contrôle des mauvaises herbes. Par conséquent, les populations sont moins nombreuses au printemps et la plupart des plantes se trouvent à l`état végétatif. La différente dynamique des populations de *S. vulgaris* résulte en une dynamique différente de *P. lagenophorae* dans le habitats rudéraux et agricoles. Dans l`habitat rudéral, la rouille a déjà été observée au mois d`avril alors qu`on ne la trouve pas avant le mois d`août dans l`habitat agricole. Ceci indique que la rouille hiverne dans l`habitat rudéral sous forme de mycélium dans son hôte alors qu`elle ne peut hiverner dans l`habitat agricole au vu de faible nombre d`hôtes hivernants. En comparaison avec l`habitat rudéral, les épidémies printaniéres de rouilles dans l`habitat agricole semblent non seulement être empéchées par la faible quantité d`inoculum mais aussi par une majorité de plantes se trouvant dans un jeune stade. Cependant, dans le deux habitats, les plantes au stade reproductif sont plus sensible envers l`infection par la rouille que les plantes à l`état végétatif. La manipulation de la dynamique de l`hôte au travers de l`hiver pour favoriser les épidémies de rouille pourrait par conséquent être utilisée comme moyen de contrôle biologique. Les *S. vulgaris* hivernant pouvant servir non seulement de source d`inoculum au printemps mais fournissant aussi des stades de développement sensibles à la rouille, ce qui favoriserait le développement des épidémies de rouille.

La plasticité phénotypique et la différentiation génétique de *S. vulgaris* provenant d`habitats rudéraux et agricoles ont été examinées lors d`une expérience en serre (chapitre 3). Les caractèristiques végétatives et reproductives des plantes des habitats rudéraux et agricoles confrontés à un milieu nutritif riche et pauvre, ainsi que se trouvant confronté ou non à l`infection par la rouille ont été comparées. Il est à signaler que les plantes de habitats rudéraux et agricoles sont génétiquement différentes. Les plantes de l`habitat agricole se caractérisent par une surface foliaire importante ainsi qu`une reproduction élevée. Leurs caractéristiques reproductives sont aussi plus plastiques face à un apport nutritif élevé. Ces résultats indiquent que la différentiation génétique entre les habitats repose sur les différences dans l`apport nutritif. Dans l`habitat agricole, là oú les populations de *S. vulgaris* sont gênées par les mesures de culture, une reproduction plus élevée pourrait être un avantage. La réserve de semences est pour *S. vulgaris* de moindre importance et c`est pour cette raison que les populations doivent s`établir à nouveau par recolonisation. Une reproduction plus élevée

augmente aussi la dispersion des semences de maniére à ce que *S. vulgaris* soit capable de s`établir rapidement dans de nouveux endroits appropriés. Des famille de *S. vulgaris* génétiquement différentes ont été trouvées seulement dans l`habitat agricole. La plasticité des caractéristiques reproductives en réponse à un apport nutritif plus élevé ont été aussi génétiquement différentes entre des familles se trouvant dans l`habitat agricole. Par contre, une différentiation génétique par rapport à l`infection avec la rouille n`a pu être démontrée. D`autre part, les plantes soumises é un apport nutritif élevé ont présenté une réaction plus forte en réponse à l`infection avec la rouille. Cette derniére a eu pour conséquence une diminution da la surface foliaire, de la biomasse végétative et de la reproduction. Par contre, il n`y a eu aucune différence entre les réactions envers l`infection entre les différentes familles rudérales et agricoles. Ceci indique que *P. lagenphorae* n`est présentement pas un important facteur de sélection pour les populations de *S. vulgaris*. L `inoculation avec succés des différentes familles avec une seule lignée de rouille montre le potentiel de ces lignées comme organismes de contrôle biologique.

Une expérience de transplantation réciproque de semences a permis d`étudier les variations génétique ainsi que celles dues à l`environnement sur le caractéristiques de vie de *S. vulgaris* provenant d`habitats rudéraux et agricoles ainsi que leur potentiel d`adaptation locale par sélection naturelle (chapitre 4). La germination, la croissance et la fertilité ont été déterminées selon les variations environnementales et génétiques. Aucune indication d`adaptation locale n`a toutefois pu être établie. La survie des plantes germinales jusqu`à la reproduction n`a été influencée que par les facteurs environnementaux, ce qui souligne l`importance des facteurs stochastiques pour la mortalité des plantes. Les plantes provenant des endroits rudéraux présentent une croissance réduite, produisant par contre des semences et se comportant par conséquent comme des plantes tolérantes au stress. Les plantes se développant dans la majorité des endroits agricoles agissent comme stratéges rudéraux, pouvant utiliser un environnement productif pour une croissance rapide et une production maximale de semences. L`établissement des plantes germinales, la survie, la croissance ainsi que la fertilité sont élevées dans les endroits agricoles par rapport à les endroits ruderaux. L`infection avec *P. lagenophorae* a été présente dans tous les endroits, avec le taux d`infection le plus élevé dans les endroits agricoles. Il a été remarqué qu`en présence de l` hôte approprié, l`infection est uniquement dépendante des bonnes conditions environnementales. Un taux d`infection plus élevé n`a toutefois pas eu comme conséquence un taux de maladie plus élevé sur la croissance et la reproduction des plantes. Cela n`a non plus pas influencé la survie de *S. vulgaris* par rapport à l`infection avec la rouille, ce qui inidique que *P. lagenophorae* n`est pas un facteur de mortalité important pour les populations de *S. vulgaris*. Tous les autres caractéristiques de vie corroborent les conditions pour la sélection naturelle. Cela donne donc à penser que *S. vulgaris*, en absence de facteurs de mortalité stochastiques, a le potentiel d` adapter à son environnement local.

Finalment, les résultats obtenus durant cette thése ont été résumes et discutés du point de vue du contrôle biologique de *S. vulgaris* en général et en particulier du point de vue de l`approche dite “system mangement”, ainsi que de la suite à donner de cette étude (chapitre 5). Comme la variation génétique de *S. vulgaris* par rapport a l`infection avec la rouille n `a pu être démontrée et comme la rouille semble présentement être un facteur de sélection mineur, les résultats soulignent le potentiel de l`approche dite “system management” pour le contrôle biologique de *S. vulgaris*. Cette méthode est conçue pour stimuler les épidémies de *P. lagenophorae* sur *S. vulgaris*, ce qui peut être atteint par les mesures suivantes i) l`hivernage de *S. vulgaris* infectées comme source d`inoculum, ii) l`utilisation de lignées unique de rouille, l`optimisation des conditions d`infection par arrosage et amendement lors de l`application de l`inoculum.

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1981	Matriculation
1982-1984	Undergraduate studies in Agriculture at the University of Bonn, Germany
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1986	Practical at the Agricultural University Wageningen, Netherlands
1986-1988	Graduate studies in Agriculture with specialisation in Crop Production at the University of Bonn, Germany
1988	Graduate Agricultural Engineer. Thesis: Untersuchungen zur *in-vitro* Regeneration und *ex-vitro* Bewurzelung von *Rubus idaeus* L.
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