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

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Abstract *Senecio vulgaris* from ruderal habitats may colonise crop fields and persist in the new environment. Persistence may occur through phenotypic plasticity or genetic differentiation. In the presence of genetic variation, differential responses 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, as shown by a significant site and origin effect. However, there was no evidence of local adaptation, as indicated by the absence of significant origin by site interactions. Genetic variation in emerging seedling numbers seems to be important for *S. vulgaris*, an annual plant which has no means other than seed production for propagation. 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* is following the plastic strategy of a stress tolerator to endure unfavourable environments. Plants at most agricultural sites behaved like *r*-strategists, exploiting a productive environment for rapid plant growth and 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 on plant growth and reproduction nor did it affect survival of *S. vulgaris*. Although the majority of life-history traits studied showed phenotypic and genetic variation, which can both be subject to natural selection, no adaptation of *S. vulgaris* to its local environment was detected.

Keywords Adaptation · Environmental and genetic variation · *Puccinia lagenophorae* · Reciprocal transplant · *Senecio vulgaris*

Introduction

Plants from ruderal habitats colonising crop fields face new environmental challenges. Agricultural habitats differ from natural/ruderal habitats due to human activity, e.g. 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 responses 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 selection over the complete plant life-cycle (Van Groenendael 1985). However, relatively few evolutionary studies have 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). In particular, emergence and growth at early stages are often not studied, although the importance of events occurring at the seedling stage for plant fitness has been emphasised (Harper 1977).

The reciprocal transplant technique is considered to be the classical method for the analysis of variation in life-history traits and the adaptive significance of genetic

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differentiation (Rapson and Wilson 1988; Schmid 1992). If resident individuals consistently outperform 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 common groundsel, *Senecio vulgaris* ssp. *vulgaris* var. *vulgaris* (Asteraceae), from ruderal and agricultural habitats. *S. vulgaris* occurs in both ruderal and agricultural habitats. It is considered an annual weed in horticulture, orchards and plant nurseries (Holm et al. 1997). 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 has probably 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* via a negative impact on plant growth and reproduction as well as causing increased plant mortality (Paul and Ayres 1986a, 1986b, 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). 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:

1. Are the life history traits emergence, survival, growth and fecundity in *S. vulgaris* determined by environmental and/or genetic variation?
2. Are ruderal and agricultural *S. vulgaris* adapted to their local environment and if so, does adaptation occur for all life history traits?
3. Is the rust fungus *P. lagenophorae* an important biotic factor with respect to the local adaptation of *S. vulgaris*?

Materials and methods

Field sites

Three *S. vulgaris* populations each for the ruderal and the agricultural habitat types 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:

1. Arconciel: an area of 13×13 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*.
2. Courtepin: an area of 5×18 m waste ground with a compacted, shallow sandy soil, which quickly drains. Vegetation is sparse with *S. vulgaris*, *Conyza canadensis* and *Eragrostis minor* being the main components.
3. Müntschemier: an area of 3×22 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, which is dominated by *Trifolium repens* and *Polygonum avicolare*.
4. Coussiberle: a vegetable plot of 4.5×60 m, planted with cabbage. The soil is a sandy loam. The site is regularly fertilised and watered sporadically.
5. Corjolens: a vegetable plot of 4×25 m, planted with leeks. The soil is a sandy loam. The site is regularly fertilised and irrigated.
6. Praz: a vineyard of about 3,800 m^2 situated in a plain on sandy loam. The site is regularly fertilised with no irrigation.

Reciprocal seed transplant experiment

Seeds of each origin were sown into a 1.50×6.00 m plot established at each site. Each plot contained six replicated seeds with 6 sites×6 origins×5 families×6 replicates=1080 seeds per site. Seeds were completely randomised within each plot. Germination of *S. vulgaris* is induced by light and can be inhibited under shade conditions (Frantzen and Hatcher 1997 and references therein). To facilitate germination and to prevent contamination with invading *S. vulgaris* seeds, the vegetation in all plots, as well as a surrounding strip of about 0.5 m, was removed prior to sowing, plots and surrounding strips 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 1×1 cm. 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, with all unmarked plants being removed regularly. 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 from 6 August to 16 November 1998.

Measurements

Various characters were measured twice a week, starting 1 week after sowing: emergence of seedlings (unfolding of cotyledons), plant survival, plant height (length in centimeters 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 milligrams), time to the onset of reproduction, plant height at onset of reproduction and number of capitula.

Data analysis

Data analysis was based on the effects of origin, representing genetic variation, and site, representing environmental variation. A significant 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. 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 1994):

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

where y is the fraction of plant height at onset of reproduction, b is a shape parameter, t is the time in days, and τ is the mid-height time, i.e. the 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 one to six replicated plants.

The effects of origin and site on estimated growth parameters were analysed using two-way ANOVAs. The analyses were based on one to five 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, 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 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.

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 1). Seedlings from the origins Arconciel, Courtepin and Corjolens had a higher probability of emergence than seedlings from Praz. Seedlings had a significantly higher probability of emergence at all other sites than at Courtepin, and seedlings from Courtepin emerged better than all others at their home site as well as at other ruderal sites (data not presented). Time to emergence showed strong environmental control, regardless of origin (data not presented).

Table 1 Effects of origin and site on seedling emergence of three ruderal and three agricultural reciprocally transplanted *Senecio vulgaris* populations analysed by logistic regression. The origin×site interaction was included in the first run of the model but was not significant in any case 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	Odds ratio (95% CI)[a]	Emergence[b]
Origin (Wald χ^2=20.92, *df*=5, *P*=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 (Wald χ^2=70.69, *df*=5, *P*<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: χ^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

Table 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 not significant in any case 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	Odds ratio (95% CI)[a]	Survival[b]
Site (Wald χ^2=12.41, *df*=5, *P*=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×site (Wald χ^2=38.10, *df*=25, *P*=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

The environment mainly determined survival of seedlings to onset of reproduction (Table 2). A significant origin×site interaction indicated that survival at the different sites was dependent on seed origin. However, the significance level for the interaction was marginal and disappeared when single outliers were removed.

Table 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*	*P*
b	Origin	5	0.55	2.14	0.067
	Site	5	6.44	25.11	<0.001
	Origin×Site	24	0.19	0.73	0.809
	Error	98	0.26		
τ	Origin	5	83.86	4.88	0.001
	Site	5	202.45	11.77	<0.001
	Origin×Site	24	19.55	1.14	0.320
	Error	98	17.20		

[a] $y=1/(1\{1+\exp[-b\times\ln(t/\tau)]\})$, in which y is the fraction of plant height at onset of reproduction, b is a shape parameter, t is time in days, and τ is the mid-height time, at which $y=0.5$

Plant growth differed between seed origins as well as sites. While the shape parameter *b* was only environmentally determined, the mid-height time τ was environmentally as well as genetically determined (Table 3). Plants originating from the ruderal site Courtepin took longer to reach the mid-height time than the other origins except those from the ruderal site Arconciel (Table 4). Plants grown at the agricultural sites Coussiberle and Corjolens had steeper shape parameters than at the other sites. Corjolens also had the shortest time to mid-height.

All traits related to reproduction were determined by environmental as well as genetic variation (Table 5). Plants of the agricultural origin Coussiberle had one of the shortest pre-reproductive periods, obtaining maximum plant size, maximum number of capitula and biomass at their home as well as at alien sites (Table 6). Plants from the ruderal origins 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 were the first to reproduce with the tallest plants, the highest number of capitula and biomass. Plants at Courtepin were the last to reproduce with the shortest plants and the minimum number of capitula and biomass.

Table 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 1–5 families with 1–6 replicated plants per family

Parameter	Ruderal populations				Agricultural populations			
	Arconciel	Müntschemier	Courtepin	Average	Coussiberle	Corjolens	Praz	Average
Origin								
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	46.3 a	45.7a	46.1
Site								
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

[a] $y=1/(1\{1+\exp[-b\times\ln(t/\tau)]\})$, in which y is the fraction of plant height at onset of reproduction, b is a shape parameter, t is time in days, and τ is the mid-height time, at which $y=0.5$

Table 5 ANOVA of vegetative and reproductive traits for three ruderal and three agricultural reciprocally transplanted *S. vulgaris* populations

Trait	Source	*df*	Mean Square	*F*	*P*
Time to reproduction (days)	Origin	5	218.05	3.40	0.007
	Site	5	662.26	10.35	<0.001
	Origin×Site	24	68.38	1.07	0.392
	Error	98	63.96		
Height at reproduction (cm)	Origin	5	87.76	3.40	0.007
	Site	5	1051.67	40.77	<0.001
	Origin×Site	24	13.38	0.52	0.966
	Error	98	25.80		
No. capitula	Origin	5	1139.49	2.98	0.015
	Site	5	20117.14	52.56	<0.001
	Origin×Site	24	223.70	0.58	0.934
	Error	98	382.74		
Biomass[a] (g)	Origin	5	0.20	2.97	0.015
	Site	5	4.35	64.39	<0.001
	Origin×Site	24	0.031	0.46	0.983
	Error	98	0.068		

[a] Data were log-transformed

Table 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 1–5 families with 1–6 replicated plants per family

Trait	Ruderal populations				Agricultural populations			
	Arconciel	Müntschemier	Courtepin	Average	Coussiberle	Corjolens	Praz	Average
Origin								
Time to reproduction (days)	83.8b	76.2a	80.6ab	80.2	76.0a	78.7ab	75.8a	76.8
Height at reproduction (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								
Time to reproduction (days)	83.8c	79.2bc	84.3c	82.4	74.6ab	71.2a	83.3c	76.4
Height at reproduction (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 for analysis. Untransformed means are shown in the table

Table 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 not significant in any case 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	Odds ratio (95% CI)[a]	Incidence[b]
Site (Wald $\chi^2=58.61$, $df=5$, $P<0.001$)		
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: $\chi^2=91.942$, $df=5$, $P<0.001$		

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

Rust infection occurred at each site with rust incidence being solely influenced by the environment (Table 7). The lowest incidence was recorded at the ruderal site of Courtepin and and compared to this site the probability of infection at all other sites was significantly higher.

Discussion

This study demonstrated both environmental and genetic variation in various life-history traits related to plant fitness, which is a prerequisite for natural selection to occur (Endler 1986). As *S. vulgaris* is established in different environments it is expected to have adapted to these either through phenotypic plasticity or genetic variation, which can both be subject to selection. Survival was the only trait exclusively under environmental control. However, adaptation of *S. vulgaris* to its local environment was not detected, as indicated by the absence of significant origin×site interactions. Similar instances of non-adaptation have been reported for *Agrostis capillaris* L. (Rapson and Wilson 1988) and *Bromus tectorum* (Rice and Mack 1991).

Being an annual plant, *S. vulgaris* has no other means of propagation than seed production, emphasising the importance of the number of seedlings emerging for overall fitness. Emergence of seedlings in general was higher at the agricultural sites, which probably provided more safe sites. Emergence in a safe site has been described as a stochastic event by Harper (1977) and studies of various perennials have supported this view (McGraw and Antonovics 1983; Cheplick 1988; Rice and Mack 1991). In contrast, genetic variation in the number of seedlings emerging has been 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 higher emergence than seeds from other sites at their home site 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 treatment of seeds at all sites 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 variation in seedling survival has also been reported for other species (Antonovics and Primack 1982; Levin and Schmidt 1985; Van Groenendael 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 their own particular genotypes, 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 higher at all agricultural sites, which suggests that conditions were more favourable in this habitat, possibly due to 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 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 than 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 might have differed between plants from different origins, because non-race-specific quantitative resistance of *S. vulgaris* to infection by *P. lagenophorae* has been reported by Wyss and Müller-Schärer (1999).

Differences in growth 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 very shallow soil and a strongly compacted soil surface. Although growth was reduced, resulting in a relatively long pre-reproductive period and smaller plant size, plants of both origins reached reproduction though the number of capitula produced was lower than for other origins. These findings suggest that *S. vulgaris* is able to endure unfavourable environments, reducing both vegetative and reproductive vigour, following the plastic 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. Both sites were vegetable production sites where short-lived annual crops were being grown, leading to a relatively high level of disturbance due to agricultural cultivation practices. Furthermore, these sites were characterised by relatively favourable soil conditions including soil nutrients, and in addition Corjolens was irrigated regularly during August, while Coussiberle was watered occasionally. In such an uncertain but potentially productive environment *S. vulgaris* seems to behave like an *r*-strategist (Grime 1979), being able to exploit a favourable environment for rapid plant growth maximising seed production. In contrast, the third agricultural site at Praz was a perennial vineyard, also with favourable soil and nutrient conditions, but less disturbance through cultivation practices than at the vegetable sites. 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 a 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.

Emergence, growth and fecundity of *S. vulgaris* showed genetic as well as environmental variation. In contrast, survival of *S. vulgaris* depended only on the environment. It is therefore 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. The possibility that genetic differentiation of *S. vulgaris* may have resulted from evolutionary forces other than selection, such as gene flow or genetic drift, can, however, not be excluded. The vagaries of dispersal and genetic drift may have limited the rate at which superior genotypes are introduced and established at a particular site (Rice and Mack 1991). Selfing followed by drift has been suggested as a potentially important differentiating mechanism in inbreeding annuals (Schemske 1984). While there are no estimates of gene flow of *S. vulgaris* between habitat types at present, a high gene flow between agricultural *S. vulgaris* populations, located in distances of less than 2 km from each other, has been estimated (H. Müller-Schärer and M. Fischer, unpublished work). To further investigate the role of gene flow in *S. vulgaris* populations, molecular studies on the genetic stability of ruderal and agricultural *S. vulgaris* populations are currently under way.

This study has confirmed the importance of including early life-cycle stages in evolutionary studies: the number of emerging seedlings is an important life-history trait for *S. vulgaris*, an annual plant with no means of propagation other than seed production. While emergence, growth and fecundity of *S. vulgaris* showed genetic as well as environmental variation, survival of *S. vulgaris*, determined only by the environment, was not related to infection by *P. lagenophorae* but depended on other stochastic mortality factors. Although for the majority of life-history traits studied phenotypic and genetic variation has been shown, which can both be subject to natural selection, no adaptation of *S. vulgaris* to its local environment was found.

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