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ADAPTATION OF *SENECIO VULGARIS* (ASTERACEAE) TO RUDERAL AND AGRICULTURAL HABITATS[1]

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Adaptation of the annual plant *Senecio vulgaris* to ruderal and agricultural habitats was investigated. We expected S. *vulgaris* to be adapted to the agricultural habitat through nutrient-specific differentiation of relatively few genotypes responding to the generally high homogenous nutrient levels at the agricultural habitat caused by constant fertilization. To assess adaptation of *S. vulgaris*, vegetative and reproductive responses of seed families from various populations of agricultural and ruderal habitats, grown in the greenhouse at high and low nutrient levels, were compared. Data were analyzed with a three-level nested ANOVA based on the levels habitat, population, and family. A significant habitat effect indicated that *S. vulgaris* from ruderal and agricultural habitats were genetically different with plants from the agricultural habitat having larger leaves and a higher reproduction. A significant habitat by nutrient effect showed a stronger response of reproduction to nutrients at the agricultural habitat, suggesting that genetic differentiation among habitats is nutrient-specific. Contrary to expectations, only the agricultural habitat showed genetic diversity of *S. vulgaris.* Results suggest that nutrient levels at the agricultural habitat are more heterogeneous as generally proposed leading to a relatively high genetic variation.

Key words: adaptation; agriculture vs. ruderal; Asteraceae; genetic differentiation; nutrients; *Puccinia lagenophorae*; *Senecio vulgaris.*

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, Scott, and Holliday, 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, fertilizer inputs, and other environmental characteristics (Barrett, 1988; Warwick, 1990). Constant inputs of fertilizer 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 Mihaliak (1986). 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 ptycanthum* from ruderal and agricultural habitats. The question of nutrient-specific differentiation in response to increased soil nutrients levels at the agricultural habitat still remains open.

Increasing environmental variability on a small spatial scale favors 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 at 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 at 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 microsites have been reported by Abbott (1976b), 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. We hypothesise that in the first case most genotypes will survive at the agricultural habitat, while in the second case only those genotypes will survive that derived from a microsite with a similar environment to that of the agricultural habitat. In both cases, low genetic variation at the agricultural habitat has to be expected. In addition, genetic bottlenecks during colonization, self-fertilization, and selective effects of agricultural practices such as chemical weed control may have further reduced genetic variation at the agricultural habitat (Barrett, 1988).

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 horticultural sites, 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

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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). The influence of nutrients on *S. vulgaris* has been investigated by Paul and Ayres (1986a). Genetic differentiation of *S. vulgaris* has been reported either by comparing plants from a single site within a botanic garden (Briggs and Block, 1992), by comparison of plants from various natural sites (Abbott, 1976a, b) and by comparing plants from natural sites with plants from botanic gardens and field margins (Theaker and Briggs, 1993). Populations of *S. vulgaris* from ruderal and agricultural habitats have not been compared yet. Comparing *S. vulgaris* from these habitats, nutrient-specific differentiation of *S. vulgaris* at the agricultural habitat was expected in response to high homogenous nutrient levels, while phenotypic plasticity was expected of *S. vulgaris* at the ruderal habitat in order to adapt to the heterogeneous nutrient levels of this environment.

The rust fungus *Puccinia lagenophorae* is the most important pathogen infecting *S. vulgaris* (Frantzen and Hatcher, 1997). Rust infection inhibits growth and reproduction of *S. vulgaris* and increases its mortality (Paul and Ayres, 1986b, c, 1987). The negative impact of the rust is enhanced on *S. vulgaris* grown at high nutrient levels (Paul and Ayres, 1986d), and the impact of *P. lagenophorae* on *S. vulgaris* might be stronger at the agricultural habitat compared to the ruderal one due to the relatively high nutrient levels at the agricultural habitat. If so, genetic differentiation of *S. vulgaris* in response to the stronger impact of the pathogen at the agricultural habitat may have occurred.

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* at 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), representative for the major occurrence of *S. vulgaris*, were sampled in the districts Fribourg and Valais of Switzerland in October 1996. The agricultural populations comprised annual and perennial crops (Table 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 minimize maternal effects, seed families were grown for one generation in a heated greenhouse, selfed, and the resulting seeds used in the experiment.

Experimental treatments—Four seeds for each family were sown into 9 cm diameter pots filled with TKS 1 peat substrate (Floragard, Oldenburg, Germany). Seeds were moistened 3 and 6 d after sowing using a De Vilbiss sprayer (De Vilbiss Company Limited, Bournemouth, UK). 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 randomized complete block design without repetition (i.e., 4 pots per family per 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 the form of the slow-release fertilizer Tardit Top (Hauert, Grossaffoltern, Switzerland) 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 nitrogen and potassium, respectively, and 183 kg/ha 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 standardize treatments not inoculated, plants were also covered with plastic bags. A second inoculation was carried out 1 wk later. Pots were watered to ensure consistent soil moisture. To prevent spread of fungus from inoculated to control plants, pots were watered from below taking care not to moisten any plant parts. Before inoculation plants were treated once with a 0.5% Teknar (Andermatt Biocontrol, Grossdietwiel, Switzerland) 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 daily temperature of 24°C with a maximum of 38°C on sunny days and 19°C during night. Incident light was supplemented by high-pressure sodium lamps (type SGR, Son-T-400W [Philips, Zürich, Switzerland]) to provide 16-h daylight. Light intensity reached 199 μmol photons·m^{-2}·sec^{-1} on average with a maximum of 1002 μmol photons·m^{-2}·sec^{-1} on sunny days. The experiment was conducted from 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.

TABLE 1. Ruderal and agricultural populations used for sampling of *Senecio vulgaris* from ruderal and agricultural habitats.

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

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 (National Institute of Health, Scion Image 1.57, USA), and vegetative biomass expressed as dry mass 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 mass 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 (National Institute of Health, Scion Image 1.57, USA) determining the fraction of the total leaf area occupied by mycelium.

Data analysis—Data were analyzed 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

TABLE 2. Nested ANOVA for vegetative and reproductive characters of *Senecio vulgaris* from ruderal and agricultural habitats in response to nutrient application (N) and rust infection (R). Mean squares and significance levels are presented.

Source of variation	df	Time to cotyledon formation	Leaf area	Vegetative biomass	Time to seed set	No. capitula	No. seeds in the first mature capitulum	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	32 096.160**	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***	239 583.057***	115.290 ns	8.275***
R	1	12.920 ns	88.023***	27.981***	142.494 ns	40 255.891***	267.272 ns	4.025***
N × R	1	25.136 ns	28.263 ns	8.283***	125.600 ns	2374.238 ns	9.843 ns	0.065 ns
Habitat × N	1	25.531 ns	5.022 ns	0.096 ns	18.465 ns	10 954.009*	34.299 ns	0.444*
Habitat × R	1	0.251 ns	0.315 ns	0.070 ns	0.015 ns	5.799 ns	5.380 ns	0.003 ns
Habitat × N × R	1	10.747 ns	1.250 ns	0.009 ns	89.104 ns	10.404 ns	95.998 ns	0.020 ns
Population × N	8	6.573 ns	36.623***	1.492**	37.987 ns	1644.046 ns	82.471 ns	0.051 ns
Population × R	8	18.364 ns	16.436 ns	0.307 ns	51.704 ns	774.370 ns	77.007 ns	0.062**
Population × N × R	8	25.755 ns	5.922 ns	0.205 ns	58.088 ns	473.663 ns	63.231 ns	0.021 ns
Family × N	40	14.061 ns	7.677 ns	0.509**	26.135 ns	751.664*	148.474 ns	0.041*
Family × R	40	19.772 ns	8.783 ns	0.321 ns	32.253 ns	424.023 ns	168.879 ns	0.019 ns
Family × N × R	40	21.051 ns	8.686 ns	0.258 ns	41.852 ns	367.523 ns	158.252 ns	0.023 ns

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; ns, not significant.

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 indicates 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 analyzed 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 characterize 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 an F ratio (Manly, 1994).

RESULTS

Vegetative and reproductive characters of *S. vulgaris* differed significantly between habitats, nutrient, and rust treatments (Table 2). Leaf area, 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. Plants from the agricultural habitat had a larger leaf area with on average 7.61 cm^2 compared to 5.41 cm^2 from plants at the ruderal habitat, and leaf area increased significantly with addition of nutrients. Plants from

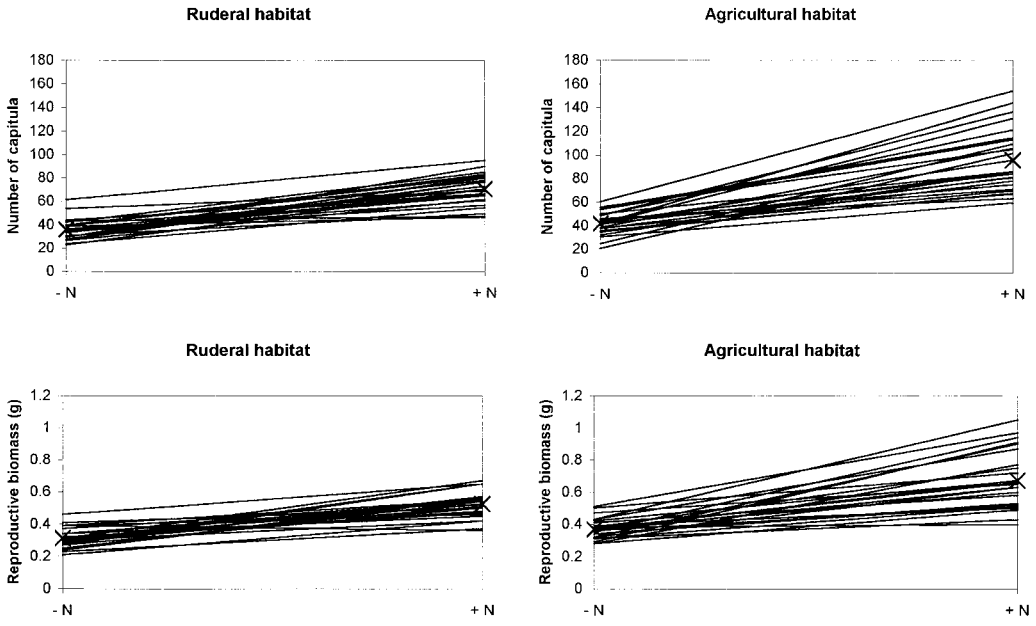

Fig. 1. Reaction norms of reproductive characters for 25 *Senecio vulgaris* families from ruderal and agricultural habitats grown with (+N) and without (−N) additional nutrients. The mean reaction norm is indicated by ×.

TABLE 3. Means and standard errors of reproductive characters of *Senecio 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 three times.

Reproductive character	Ruderal habitat				Agricultural habitat			
	−N	+N	−R	+R	−N	+N	−R	+R
No. 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
Reproductive 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

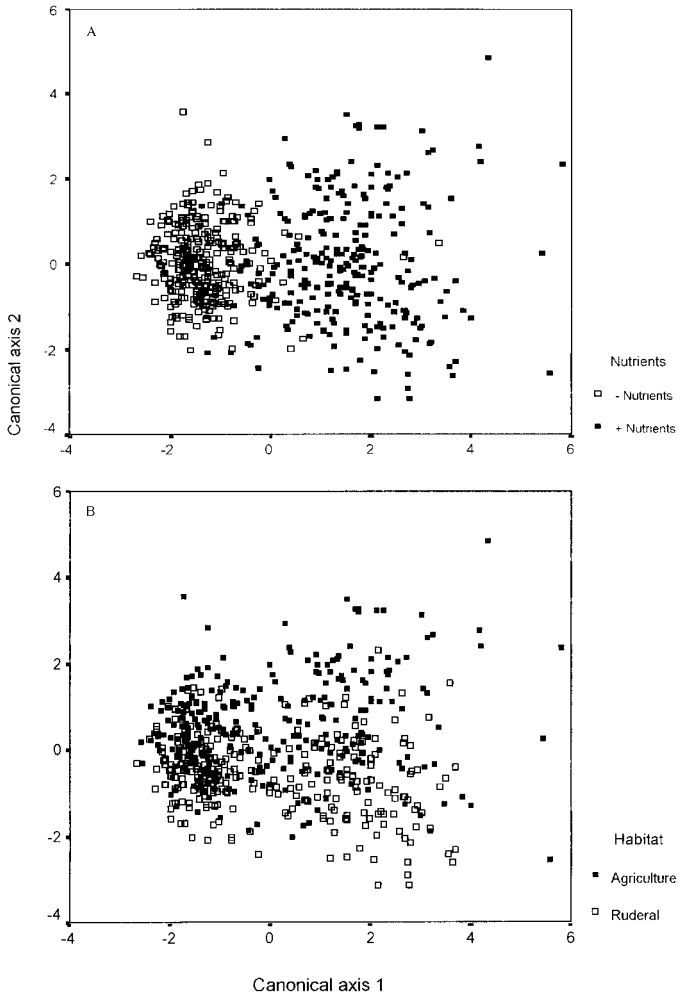

Fig. 2. Canonical discriminant analysis separating *Senecio vulgaris* from ruderal and agricultural habitats grown at two nutrient and two rust levels. Due to the high concentration of data points, separation along the first canonical axis into nutrient groups (A) and separation along the second canonical axis into habitat groups (B) are shown apart. Only the first two canonical axes are displayed. 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.

the agricultural habitat also produced a higher number of capitula and an increased amount of reproductive biomass compared to those from the ruderal habitat (Table 3). As expressed by the significant habitat by nutrient interactions (Table 2), additional nutrients led to a significantly higher increase in leaf area, number of capitula, and reproductive biomass at the agricultural habitat compared to the ruderal one (Fig. 1). Genetic differences among families for both number of capitula and reproductive biomass were only detected for the agricultural habitat (Table 4). Agricultural families differed significantly in their reaction towards nutrient application (Fig. 1) as indicated by the significant family by nutrient interaction (Table 4). In the rust treatments all *S. vulgaris* plants from the ruderal and from the agricultural habitat were infected. Rust infection significantly decreased leaf area, vegetative biomass, number of capitula, and reproductive biomass (Table 3). The response of reproductive characters to rust infection did not differ between habitats. Only reproductive biomass differed in response to

TABLE 4. Nested ANOVA per habitat for reproductive characters of *Senecio vulgaris* from ruderal and agricultural habitats in response to nutrient application (N) and rust infection (R). Mean squares and significance levels are presented.

Source of variation	df	Ruderal habitat		Agricultural habitat	
		No. capitula	Reproductive biomass	No. 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	73 895.389***	2.463**	175 836.607***	6.213**
R	1	19 611.077**	1.912**	21 010.421**	2.143**
N × R	1	1027.160*	0.079 ns	1359.091 ns	0.007 ns
Population × N	4	918.630*	0.046**	2361.218 ns	0.055 ns
Population × R	4	868.277*	0.055*	702.277 ns	0.072 ns
Population × N × R	4	98.803 ns	0.014 ns	863.026 ns	0.029 ns
Family × N	20	240.257 ns	0.010 ns	1260.670**	0.073**
Family × R	20	217.863 ns	0.013 ns	626.943 ns	0.025 ns
Family × N × 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, not significant.

rust infection at the population level (Table 2) and here only among ruderal populations (Table 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 2) and number of capitula (Table 4).

Plants of *S. vulgaris* from ruderal and agricultural habitats could be distinguished by canonical discriminant analysis (Fig. 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 (Fig. 2A), while the second axis separated habitats (Fig. 2B). 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, separating the groups with and without rust infection, 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 5). The distance between groups with and without nutrient application at the agricultural habitat was higher than that for the ruderal habitat, indicating a stronger overall plastic response to nutrients at the agricultural habitat (Table 5A). Overall, phenotypic plasticity to rust infection was substantially lower than that to nutrient application (Table 5B). The distance between groups with and without rust infection at 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 *Senecio vulgaris* from ruderal and agricultural habitats were genetically different. 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 fertilization and plants of these habitats seem to be able to translate these higher nutrient levels into an increased reproductive output.

These results are in contrast to the study of Hermanutz and Weaver (1996) comparing *Solanum ptycanthum* of ruderal and agricultural habitats. They detected neither genetic differences associated with nutrient availability nor divergence in the amount of overall plasticity to nutrients. Also, Blais and Le-

TABLE 5. Mahalanobis distances of the canonical discriminant analysis separating *Senecio vulgaris* groups from ruderal and agricultural habitats grown (A) with (+) and without (−) additional nutrients and (B) with (+) and without (−) rust infection. Significant differences in Mahalanobis distances, implying distinction among groups, were tested using an *F* ratio.

A Groups	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***	—
B Groups	**Ruderal/+Rust**	**Rudral/−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***	—

*** $P \leq 0.001$.

chowicz (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. In *Stellaria media,* greater production of seed at the higher soil fertility was based on an 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 nonweeded sites has been reported (Kadereit and Briggs, 1985; Briggs and Block, 1992; Theaker and Briggs, 1993).

An increased reproductive output might also be of advantage for *S. vulgaris* at the regularly disturbed agricultural habitat. Seeds of *S. vulgaris* have a low degree of dormancy, generally germinating immediately, and seeds that do not germinate show a relatively short period of survival in the soil (Popay and Roberts, 1970; Roberts and Feast, 1972). With the soil seed bank being of minor importance reestablishment of agricultural *S. vulgaris* populations may occur through colonization, requiring dispersal of *S. vulgaris* seeds from adjacent field margins or neighboring 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 resembling a metapopulation of which the subpopulations 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 adaptation of *S. vulgaris* plants to this heterogeneity enabling them to quickly reestablish new patches at favorable sites. The results obtained can now be used in a reciprocal transplant experiment to demonstrate adaptation of *S. vulgaris* in the field.

Contrary to expectations, the agricultural habitat 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. In general the agricultural habitat is area-wise larger than the ruderal habitat and, especially if viewed as a group of weed patches in various crops being connected by seed dispersal, nutrient levels within the agricultural habitat will be variable. The more varied genotype composition at the agricultural habitat is therefore likely to be related to gene flow among subpopulations exploiting 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 (1986d) 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 agricultural habitat.

In colonizing the agricultural habitat, *S. vulgaris* seems to have adapted to the higher nutrient levels of this habitat through differentiation of genotypes with a relatively 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 at the agricultural habitat is more varied because it also comprises genotypes with a relatively low response to high nutrient levels. The present study suggests that, although nutrient levels at the agricultural habitat are higher, they are not as homogenous as generally proposed and that the more varied genotype composition is related to gene flow among subpopulations exploiting sites with different levels of nutrients within the habitat. Thus, the agricultural habitat is not genetically impoverished as often supposed but shows higher genetic diversity than the ruderal habitat.

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