

## POPULATION DIFFERENTIATION IN THE RANGE EXPANSION OF A NATIVE MARITIME PLANT, *SOLIDAGO SEMPERVIRENS* L.

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*Solidago sempervirens*, a halophytic goldenrod native to coastal dunes and marshes of eastern North America, has expanded its range inland along roads in parts of the northeastern United States during the past 20–30 yr. This expansion has been concurrent with the application of deicing salts on roadways in winter. During the same period, the species has appeared inland along the St. Lawrence waterway and the Great Lakes of Canada and the United States and near salt mines or seeps in western and west-central New York. In a greenhouse study of nine populations from coastal Massachusetts to west-central New York, we asked whether *S. sempervirens* has a physiological dependence on salt and whether populations differ genetically with respect to ecologically important traits, such as salt tolerance, phenology, and biomass allocation. Progeny from 20 maternal families per population were subjected to three watering treatments: control (no salt), medium salt (2% salinity), and high salt (4% salinity). Phenotypic traits differed significantly by treatment, population, and population response to treatment. Total plant mass decreased in response to salt, indicating no physiological dependence on salt; the species association with saline environments may therefore result from a tolerance for salt and to low competitive ability in nonsaline habitats. The reduction in total plant mass with increasing salt primarily resulted from a decrease in average shoot mass and less to a reduction in root mass. Even so, root allocation (i.e., the allometric exponent relating root mass to shoot mass) decreased from the control to the mid- and high-salt treatments. The propensity to flower during the course of the experiment also decreased with increasing salt. Flowering propensity increased from eastern to western populations in parallel with a gradient of increasing continentality. There was also some indication that coastal populations were less tolerant of high salt than inland populations. These geographic patterns of trait differentiation may indicate adaptive divergence among populations. There was significant variation attributable to family for biomass traits, but few trait heritabilities differed significantly from zero within populations.

**Keywords:** *Solidago sempervirens*, population differentiation, range expansion, bolting frequency, salt tolerance.

### Introduction

One of the principal questions in ecology concerns the factors affecting the abundance and distribution of species (Anderwartha and Birch 1954; Hairston et al. 1960; Preston 1962; Gaston 1994; Brown et al. 1996). In plants, considerably more attention has been given to patterns and determinants of species abundance than to patterns and determinants of species distributions (Rabinowitz 1981; Brown 1984; Gaston 1996; Brown and Lomolino 1998; but Gaston 1990, 1991, 1996; Pigott 1992). Interest in range size and range limits has increased lately as a result of concerns about the effects of climate change on species distributions (Geber and Dawson 1993; Hoffman and Blows 1994) and the rapid range expansion of nonnative invasive species (Pysek et al. 1995; Starfinger et al. 1998; Enserink 1999; Lonsdale 1999).

For both native and nonnative taxa, there are three basic determinants of species range limits: climate (abiotic factors; Box 1981; Woodward and Williams 1987), biotic interactions

(Brown and Lomolino 1998), and history (Davis 1986). Both climate-controlled range edges and biotically controlled range edges imply an equilibrium between the current range and the biotic or abiotic factors that limit distribution (Box 1981). In contrast, historically determined range edges do not represent an equilibrium (Davis 1986). Rather, they are an artifact of a historical event and can be in the process of either expansion or contraction (Jacobson 1979; Pigott 1989). The colonization of new ranges by nonnative species is testimony to the importance of historical limitations on species distribution, although altered biotic interactions are thought to be important for their rapid spread in novel environments (Lodge 1993b, 1993a). A historically determined range edge is also subject to biotic and abiotic influences, and ultimately the balance of these three factors and the evolutionary potential of expanding populations will determine the eventual limits to the species distribution.

Any species that expands its range to move beyond its original habitat is ecologically interesting because the balance of biotic and abiotic factors in the new area may be different than in the original habitat. It is of particular interest to study populations at different points in an expanding range in order to learn whether they have diverged in ecologically important

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traits (e.g., phenology), and if so, whether phenotypic variation parallels environmental gradients. Because phenotypic divergence in association with environmental gradients may be indicative of adaptive evolution (Endler 1977), such evidence is germane to debates on the importance of migration versus adaptation in species responses to environmental change and on the genetic limits to range expansion (Antonovics 1976; Bradshaw and McNeilly 1991; Geber and Dawson 1993; Hoffman and Blows 1994; Garcia-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997). While there is ample evidence of geographic (and ecotypic) variation across the native range of plant species (Turesson 1922; Clausen et al. 1948; Linhart and Grant 1996; Jonas and Geber 1999) as well as evidence of differentiation among populations of invasive species in their new range (Reinartz 1984; Rice and Mack 1991a, 1991b, 1991c; Weber and Schmid 1998; Pappert et al. 2000), there is very little information on population variation in native species whose range or habitat is expanding.

A well-documented example of native species range expansion is the inland movement along roadsides of herbaceous coastal plants both in northern Europe and North America (Mathews and Davison 1976; Catling and McKay 1980; Scott and Davison 1982, 1985). In the past several decades, species that are established members of the coastal community have begun to appear along inland roadsides in regions where deicing salts are applied to roads in winter. Presumably, these species are able to exploit the new roadside habitat because of the saline environment created by deicing salt and the gaps resulting from salt damage to existing roadside vegetation (Scott and Davison 1982, 1985).

Our study focuses on *Solidago sempervirens* L. (Asteraceae), a herbaceous perennial native to sand dunes and marshes along the North American Atlantic and Gulf Coasts. *Solidago sempervirens* has been shown to be highly tolerant of both soil salinity and airborne salt spray (Oosting 1945; Cartica and Quinn 1980; Orava and Drake 1997). Its north to south range spans from Nova Scotia, Canada, to the Caribbean Gulf Coast, with the presence of a northern (*S. sempervirens* var. *sempervirens*) and a southern (*S. sempervirens* var. *mexicana*) subspecies (Lamont 1994). Its distribution in the dune community is well studied (Koske and Halvorson 1981; Lee 1995). Inland populations of *S. sempervirens* have been found along the St. Lawrence waterway in Quebec, Canada (Fillion and Salmon 1983) along the Great Lakes of Canada and the United States (Swink 1969; Swink and Wilhem 1979; Catling and McKay 1980; Innes and Hermanutz 1988; Lamere 1991), with the first reports from Chicago in 1969 (Swink 1969). In 1981, an inland population was also found at the southern tip of Seneca Lake, in the Finger Lakes region of west-central New York (Watkins Glen, N.Y.; R. Wesley, personal communication). In the past 20–30 yr, the inland spread of *S. sempervirens* from coastal northeastern United States has been documented along highways in New Jersey, Pennsylvania, New York, Connecticut, and Massachusetts (Mehrhoff 1996). Inland populations are associated with railroads and industrial zones, roadways, brine wells and salt-mining activity, or marshes. We chose to study *S. sempervirens* because it allowed us to compare plants from populations along an expanding species range.

Our first question was whether *S. sempervirens* has a physiological dependence on salt. If it does, then its recent expan-

sion and persistent association with saline environments would be attributable to this salt dependence. If *S. sempervirens* actually grows better in the absence of salt, then its association with saline environments is presumably the result of a greater tolerance of salt relative to other species, and its recent expansion may be the result of elimination of nontolerant but more competitive plants from roadsides.

Second, we asked whether populations along the expanding range differed genetically with respect to ecologically important traits, such as salt tolerance, phenology, and resource allocation. Population divergence could be due to genetic drift from founder effects in colonizing populations (Nei et al. 1975). Alternatively, population divergence may be adaptive. Adaptive differentiation would be most evident if phenotypic traits changed in association with geographic location or habitat.

Third, because the potential for adaptive differentiation depends on the existence of within-population genetic variation, we also were interested in assessing levels of population genetic variation for ecologically important traits.

## Material and Methods

### Seed Collection

We collected *Solidago sempervirens* seeds from nine sites during November and December 1999. Two sites (A, B) were typical coastal populations (southern coast and Cape Cod, Mass.); three (C–E) were collected along Interstate 84 in central Massachusetts, central Connecticut, and eastern New York; and four populations (F–I) were collected in the vicinity of Watkins Glen in west-central New York (fig. 1). Population F, one of the aforementioned inland populations, was discovered in 1981 along the roadside near a salt mine, and G–I are more recent populations expanding outward from this source. These nine sites were chosen to represent part of the east-west range of *S. sempervirens* including typical native-habitat (coastal A, B) and inland-roadside sites (C–E, F–I).

In each of the nine populations, seeds were collected from 20 plants separated by a minimum of 5 m (for a total of 180

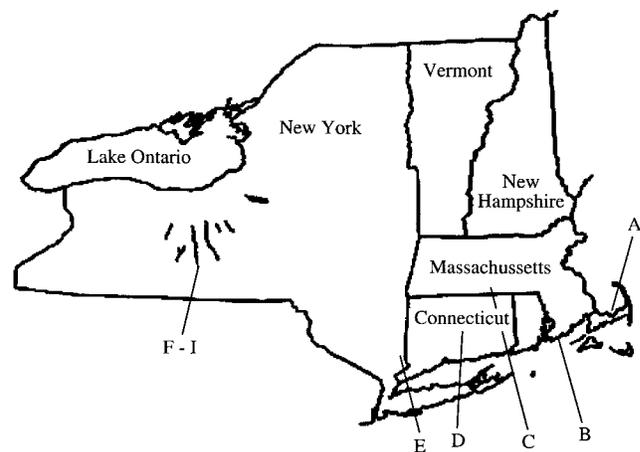


Fig. 1 Geographic location of the nine populations of *Solidago sempervirens* in the northeastern United States.

maternal families). This separation between collections was sufficient to ensure that maternal plants were genetically distinct individuals because unlike other *Solidago* species, *S. sempervirens* does not spread extensively from underground rhizomes (Duncan and Duncan 1987), and it is self-incompatible (Goodwin 1937; Innes and Hermanutz 1988). The seeds were stored at room temperature.

#### Field Survey

From July 16 to July 20, 2000, we revisited the original nine seed collection sites and characterized each site by noting the area covered by the population and estimating the density and census size of the population. We also identified co-occurring plant species and noted whether they were native or nonnative weedy species and whether they were coastal halophytic species, noncoastal halophytes, or nonhalophytes based on information in Gleason and Cronquist (1963). We define halophytes as species that are often, though not necessarily, restricted to saline environments.

#### Germination and Establishment of Experimental Plants

On December 17, 1999, we placed 40 seeds from each maternal plant into cold stratification at 5°C for 6 wk. After cold stratification, the seeds were germinated in a climate-controlled growth chamber (18-h days, 60% RH, 20°C). The seeds began to germinate after 24 h and continued to germinate for 3 wk. We planted seedlings into 4.5 × 4.5-cm flats filled with Metro Mix 360 (Scotts-Sierra Horticultural Products, Maryville, Ohio). Except for maternal seed families with insufficient germination, 12 seedlings were planted per family. For maternal families with fewer than 12 germinants, all seedlings were planted. The seedlings were then transferred to a climate-controlled greenhouse illuminated with 400-W high-pressure sodium bulbs. Temperature in the greenhouse ranged from 18°–32°C. While in the flats, the seedlings were watered twice daily with tap water to maintain a consistently damp medium.

From March 26 to March 29, 2000, we transplanted six haphazardly selected seedlings from each maternal family to 15-cm-diameter pots filled with OilDri fritted clay (Softco Mead, Elmira, N.Y.). This medium was chosen because it drains as well as the sandy soil of the natural habitat, but retains water better and allows for easy root extraction at the end of the experiment. Additionally, it does not accumulate salt and cause a buildup of salinity. At this stage, we excluded eight maternal families from the experiment because they had fewer than three surviving seedlings (not enough to receive all three salt treatments). Eight maternal families with three to five surviving seedlings were included in the experiment, and three seedlings were transplanted. Thus, they received all treatments but had no replication within treatments. This left 164 families with complete replication.

For 2 wk after transplanting, we watered the plants daily with clear tap water, supplemented once a week with a dilute nutrient solution (EXCEL 15-5-15 plus micronutrients). This pretreatment interval allowed the plants to become sufficiently well established to withstand salt stress without high early mortality. While it is important to understand the effect of salinity on all life stages of *S. sempervirens*, expected high

mortality in the early stages made it impractical to test all life stages in one experiment.

#### Experimental Design

The experiment was designed to distinguish family and population-level variation of phenotypic traits in response to salt. To this end, the seedling families from each of the nine populations (172 total families) were subjected to three watering treatments: control (no salt), medium salt (2% salinity), and high salt (4% salinity). We chose these salinity concentrations to bracket the salinity of seawater (3%; Orava and Drake 1997). Two plants from each maternal family were assigned to each treatment for a total of six seedlings from each family (except where noted above).

Pots were arranged in a blocked design in the greenhouse, with a total of 10 blocks. Two maternal families per population were randomly assigned to each block. Within a maternal family, all six seedlings were placed in the same block (for a total of 108 individuals per block). Within a block, all plants assigned to one treatment were grouped together in a subplot in order to facilitate watering and minimize plant contact with other treatments (three subplots per block; 36 individuals per subplot). The position of treatment subplots within a block was random.

#### Treatment

On April 16, 2000, we began treating the plants with salt. The control plants received pure tap water with dilute nutrient solution (EXCEL 15-5-15 plus micronutrients). The medium- and high-salt treatment groups received an identical nutrient solution with 2% or 4% salt content (weight/volume). The salt used to make the solutions was Diamond Crystal WinterMelt De-Icing Crystals (Cargill, Minneapolis). Plants were watered daily by hand to capacity. Five days per week plants received the appropriate treatment, and twice weekly they were watered with pure tap water to prevent salt buildup on the leaves or in the soil. This interval of flushing was chosen to simulate approximately natural salt leaching from soils by rainstorms.

#### Harvest

Plants were harvested from June 12 to June 16, 2000. At this time, we noted whether or not the plants had bolted (initiated an inflorescence). Plants were separated into root tissue and shoot tissue, which were dried at 70°C and weighed. Since the harvest took several days, blocks were harvested in random order. This allowed us to factor out any additional growth of plants harvested later as part of the block effect.

#### Analysis

We analyzed the effects of treatment, population, and family on total plant mass, root mass adjusted for shoot mass, and the frequency of bolting. Because final plant height was highly positively correlated with total plant mass and root and shoot mass were themselves highly correlated, we chose total plant mass as a measure of plant performance. The relationship of root mass to shoot mass was used as a measure of below versus above ground resource allocation, and the frequency of plants

that bolted measured the propensity of plants to flower during the course of the experiment. Variation in bolting frequency, as measured in this study, could reflect true differences in reproductive allocation or simply differences in the timing of flowering within a season. In other words, it is possible that plants that had not bolted by harvest time would have eventually done so if the duration of the experiment had been extended.

Analyses of total plant mass and root mass were performed on measurements taken from each plant. Bolting frequency was calculated as the proportion of individuals from each family, population, treatment, and block that produced an inflorescence. Because there were only two replicate plants per family and population in each treatment and block, bolting frequency could only take on values of 0, 0.5, or 1.

Traits were analyzed with a mixed-model analysis of variance (total mass, bolting frequency) or covariance (root mass) in which block, family nested within population and block, and interactions with block and family were treated as random effects, while salt treatment, population, and their interaction were treated as fixed factors (SAS; Littell et al. 1996). In the mixed-model analysis, random effects are estimated by restricted maximum likelihood. The significance of random effects was tested by computing the difference in  $-2$  log likelihood of a model that included the effect of interest (e.g., family nested within population and block) and a model that excluded the effect. The difference in log likelihood of the two models has a  $\chi^2$  distribution with 1 df. The fixed effects of treatment, population, and their interaction were tested by means of  $F$ -tests based on Type III sums of squares, with the treatment effect tested against the block by treatment interaction.

Total mass, root mass, and shoot mass were  $\log_e$  transformed, and bolting frequency was arcsine-square root transformed to improve homoscedasticity of variances. Because plant mass values were  $\log_e$  transformed, a statistically significant treatment by population interaction means that populations differed in the proportionate effect of salt on plant mass. In the analysis of root mass, shoot mass was included as a covariate for two related reasons. First, because root mass typically increases with shoot size in plants, an assessment of root responses independent of shoot size effects requires the use of shoot size as a covariate. Second, the analysis of total mass already addresses whole-plant size responses. An analysis of root mass, unadjusted for shoot mass, would only repeat the latter analysis. Because of the  $\log_e$  transformation of mass values, the regression slope ( $b$ ) of root mass on shoot mass in the analysis of covariance is equal to the allometric exponent in the relationship: root mass =  $a(\text{shoot mass}^b)$ . The mean values of root mass that we report for populations and treatments are adjusted for population and treatment differences in mean shoot mass.

When significant population and treatment by population effects were found, we performed preplanned contrasts to compare coastal (A and B) versus inland populations (C–I); coastal versus roadside populations in New England (C–E); and older (F) versus recent (G–I) populations at Watkins Glen, New York. When significant family effects were found for a trait, we analyzed trait variation within each population separately

to ask whether the trait was genetically variable at the population level.

## Results

### Sites

The nine seed collection sites differed in areal extent, plant density, and census population size of *Solidago sempervirens* (table 1). Many of the roadside populations were long linear strips of habitat containing *S. sempervirens*. The census population size was large at all sites (minimum of 800 plants at site I).

The sites also differed in the identity of co-occurring species. At the coastal sites, the dominant co-occurring species consisted of a mixture of native coastal halophytes, nonnative coastal halophytes, and nonnative weeds that are not halophytes. Inland sites were dominated by weedy species, many of which are not halophytes.

### Treatment Effects

There was a highly significant treatment effect on all three phenotypic traits (table 2). Plants from all populations had the highest total mass, root mass adjusted for shoot mass, and bolting frequency when grown with no salt (control) and decreasing trait values with increasing salt (table 3). Although decreases in both shoot mass and root mass contributed to the reduction in total plant mass with increasing salt, shoot-mass reductions were proportionately larger than reductions in root mass (table 3). Even so, root allocation, measured as the allometric exponent of the relationship (root mass =  $a[\text{shoot mass}^b]$ ) decreased with increasing salt (table 3). Thus, while root and shoot mass were related isometrically in the absence of salt ( $b \cong 1.0$ ), the allometric coefficient decreased by ca. 25% for each 2% increase in salt concentration.

### Population Divergence in Traits and in Trait Responses to Salt

All three phenotypic characters, averaged over the three watering treatments, differed significantly among populations (table 2; fig. 2a–2c). Contrasts between sets of populations indicated that coastal populations (A, B) differed significantly from inland populations (C–I) for all three traits (table 4). The inland versus coastal differences in total mass and root mass were not significant in the absence of salt (table 4; fig. 3a, 3b). Indeed, at 0% salt, populations A and C had significantly smaller total mass than all other populations (fig. 3a), which indicates that population differences in total mass in the absence of salt cannot be attributed to a coastal versus inland phenomenon. In the presence of salt, and especially at the highest salt concentration, plants from coastal populations exhibited a greater decrease in size compared to inland populations since the percentage reduction in total mass with versus without salt was greater for coastal populations (figs. 2d, 3a; contrast between coastal and inland populations in the average percentage reduction in biomass across 2% and 4% relative to no salt:  $F_{1,140} = 5.81$ ,  $P < 0.02$ ). The latter result indicates that coastal populations may be less tolerant than inland populations of high salt levels, although, here again, the first inland

**Table 1**  
**Site Characteristics of the Nine Populations of *Solidago sempervirens***

Population	Location	Site size (m <sup>2</sup> )	Plant density (plants/m <sup>2</sup> )	Census size (m <sup>2</sup> )	Dominant co-occurring plant species
A	Cape Cod, Mass. (Sandy Neck Beach) 41.4°N, 70.2°W	2000	11.3	22,600	<i>Ammophila breviligulata</i> <sup>a,c</sup> <i>Artemisia stelleriana</i> <sup>b,c</sup> <i>Hudsonia tomentosa</i> <sup>a,c</sup> <i>Lathyrus japonicus</i> <sup>b,d</sup> <i>Myrica pensylvanica</i> <sup>a,e</sup> <i>Rosa rugosa</i> <sup>b,c</sup>
B	South Coast, Mass. (Horseneck Beach) 41.3°N, 71.3°W	800	4.3	3400	<i>Ammophila breviligulata</i> <sup>a,c</sup> <i>Cakile edentulata</i> <sup>a,c</sup> <i>Lathyrus japonicus</i> <sup>b,d</sup>
C	Sturbridge, Mass. (Jct. I-84, I-90, Rt. 20) 42.1°N, 72.0°W	1000	30.7	30,700	<i>Achillea millefolium</i> <sup>a,c</sup> <i>Carex intumescens</i> <sup>a,e</sup> <i>Erigeron canadensis</i> <sup>a,e</sup> <i>Hypericum perforatum</i> <sup>b,e</sup> <i>Linaria vulgaris</i> <sup>b,e</sup> <i>Phragmites australis</i> <sup>b,d</sup> <i>Rhus typhina</i> <sup>a,e</sup>
D	Hartford, Conn. (I-84) 41.8°N, 72.7°W	80	26.3	2104	<i>Artemisia vulgaris</i> <sup>b,e</sup> <i>Cichorium intybus</i> <sup>b,e</sup> <i>Daucus carota</i> <sup>b,e</sup> <i>Melilotus alba</i> <sup>b,e</sup> <i>Rhus typhina</i> <sup>a,e</sup> <i>Tus-silago farfara</i> <sup>b,e</sup>
E	Connecticut–New York border (I-84) 41.2°N, 73.3°W	110	44.2	4900	<i>Artemisia vulgaris</i> <sup>b,e</sup> <i>Lythrum salicaria</i> <sup>b,e</sup> <i>Phragmites australis</i> <sup>b,d</sup>
F	Watkins Glen, N.Y. (Rt. 414) 42.2°N, 76.60°W	2800	42.1	117,900	<i>Centauria maculosa</i> <sup>b,e</sup> <i>Daucus carota</i> <sup>b,e</sup> <i>Melilotus alba</i> <sup>b,e</sup> <i>Poa compressa</i> <sup>b,e</sup> <i>Rhus typhina</i> <sup>a,e</sup> <i>Solidago altissima</i> <sup>a,e</sup>
G	Watkins Glen, N.Y. (Salt Point) 42.2°N, 76.62°W	900	24.5	22,100	<i>Centauria maculosa</i> <sup>b,e</sup> <i>Cichorium intybus</i> <sup>b,e</sup> <i>Daucus carota</i> <sup>b,e</sup> <i>Melilotus alba</i> <sup>b,e</sup> <i>Poa compressa</i> <sup>b,e</sup> <i>Solidago altissima</i> <sup>a,e</sup>
H	Watkins Glen, N.Y. (Rt. 14) 42.2°N, 76.64°W	75	105.0	7900	None
I	Watkins Glen, N.Y. (Rt. 14) 42.2°N, 76.67°W	10	76.5	800	<i>Solidago altissima</i> <sup>a,e</sup>

Note. Site size estimated from linear dimensions of the site. Census size estimated as the product of site size by plant density.

<sup>a</sup> Origin: native species.

<sup>b</sup> Origin: nonnative weedy species.

<sup>c</sup> Habitat affiliation: coastal halophyte.

<sup>d</sup> Habitat affiliation: noncoastal halophyte.

<sup>e</sup> Habitat affiliation: nonhalophyte.

population C also exhibited a large percentage reduction in total mass with increased salinity (fig. 2d).

The higher average root mass (adjusted for shoot mass) in coastal versus inland populations (fig. 2b) was not due to a consistent pattern of population differentiation across all salt levels. Indeed, adjusted root mass hardly changed across salt treatments in population A (fig. 3b), whereas root mass declined in population B with increasing salt (fig. 3b) as was the case with all other populations. The statistically significant contrast between coastal and inland populations for average root mass was the result of the high root mass in population B at 0% salt, high root mass in populations A and B at 2% salt, and high root mass in population A at 4% salt (fig. 3b).

Across all treatments, there was a geographic trend in average bolting frequency with eastern populations bolting less than western populations (fig. 2c). In addition, the flowering response of populations to increasing salt differed, with the most maritime population (A) flowering least in all treatments

(fig. 3c). Population B was very plastic in its response to salt, with virtually all plants flowering in the absence of salt versus no flowering at 4% salt (fig. 3c). Moving westward, populations exhibited decreasing levels of plasticity to salt and a higher average bolting frequency (fig. 3c). Finally, there was 100% flowering in all treatments in the older population (F) at Watkins Glen (fig. 3c).

Comparisons of coastal and roadside populations in New England reflected the same patterns as the contrasts between coastal and all inland populations (table 4). There were many fewer significant trait differences among Watkins Glen populations (figs. 2, 3; table 4). Population F had higher root mass in the absence of salt and greater flowering at high salt compared to other Watkins Glen populations.

#### Random Effects

Neither the block effect nor the treatment by family interaction was significant for any of the characters (table 5). The

**Table 2**  
**F-Tests for Fixed Effects in Split-Plot Analyses of Variance or Covariance of Total Plant Mass, Root Mass, and Bolting Frequency**

Source	Total plant mass <sup>a</sup>		Root mass <sup>a,b</sup>		Bolting frequency <sup>c</sup>	
	df	F	df	F	df	F
Treatment	2, 18	529.71***	2, 117 <sup>b</sup>	27.14***	2, 18	47.70***
Population	8, 153	22.05***	8, 797	4.45***	8, 70	57.41***
Treatment × population	16, 308	4.19***	16, 736	2.18**	16, 310	4.97***
Shoot mass <sup>b</sup>	...	...	1, 925	333.51***	...	...
Shoot mass × treatment	...	...	2, 859	14.89***	...	...
Shoot mass × population	...	...	8, 864	3.86***	...	...
Shoot mass × treatment × population	...	...	16, 786	2.29**	...	...

<sup>a</sup> Total plant mass and root mass were also log<sub>e</sub> transformed for the analyses.

<sup>b</sup> Root mass was analyzed by analysis of covariance with log<sub>e</sub> (shoot mass) as the covariate. The denominator df associated with the test of the treatment effect depends on the value of the covariate where the regression lines are being compared (Littell et al. 1996). The comparison shown in this table is evaluated at the mean log<sub>e</sub> (shoot mass) across all treatments. Tests of the treatment effect are also statistically significant when the covariate is set equal to the mean log<sub>e</sub> (shoot mass) for the 0, 2, and 4% salt treatment.

<sup>c</sup> The dependent variable is the proportion of plants that bolted per treatment, block, population, and family. Bolting frequency was arcsine-square root transformed for the analysis.

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.0001$ .

block by treatment interaction was significant for total plant mass and root mass but not for bolting frequency, and the block by population interaction was only significant for bolting frequency (table 5).

There was a significant family effect on total plant mass and root mass, indicating that these traits were genetically variable (table 5). However, separate analyses of each population revealed significant heritabilities for total plant mass in only three populations, and nonsignificant heritabilities for root mass in all nine populations.

### Discussion

The most basic conclusion of our study is that *Solidago sempervirens* does not appear to be physiologically dependent on salt and, in fact, grows better in nonsaline environments as evidenced by a sharp decrease in total plant mass as salinity increased (table 3; fig. 2). While coastal dune plants generally have a higher tolerance for salt than inland species (Oosting 1945; Barbour et al. 1985), the physiological mechanism of their tolerance is often not thoroughly studied. It has been suggested that no plant is an obligate halophyte (Barbour 1970), and studies of several halophytes have shown them to grow as well or better in the absence of salt (Rozema et al.

1978; Orava and Drake 1997). This leads to the question of what causes the association of *S. sempervirens* with saline soil if salinity is actually detrimental to plants. Plant-strategy theory suggests that the traits necessary for competitive ability differ from those that confer stress tolerance and that species that are specialized to be resistant to stress often have characteristics that compromise their competitive ability (Grime 1979). Additionally, models of community structure have suggested that stresses that cause a decline in the biomass of abundant species allow for the increase in biomass of species that can withstand the stress (Tilman 1996; Ungar 1998). Thus, it is reasonable to propose that *S. sempervirens* is both salt tolerant and a poor competitor that can exploit dune and roadside environments because of the decreased competition resulting from salt-induced fitness reduction of competing species. The prevalence of weedy species, many of which are not specifically halophytic, in both coastal sites and especially in roadside sites (table 1) is consistent with the hypothesis that *S. sempervirens* is a poor competitor (Silander and Antonovics 1982; Lee 1995).

Absolute and proportionate reductions in biomass in response to salt were more pronounced for shoots than for roots in all populations. It is not clear whether this difference reflects a greater sensitivity to salt of shoots relative to roots or whether

**Table 3**

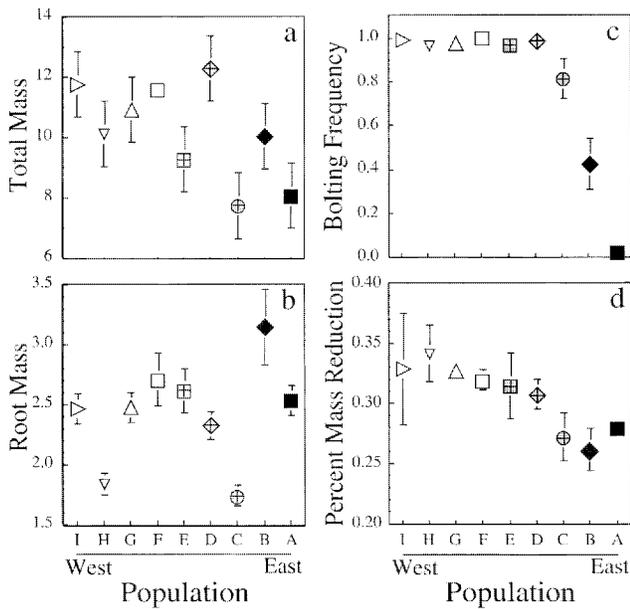
**Means ± SE of Phenotypic Traits in the Three Salt Treatments**

Trait	Total plant mass <sup>a</sup>	Root mass <sup>a</sup>	Root to shoot allometry <sup>b</sup>	Bolting frequency <sup>a</sup>
0% salt	23.27 ± 1.04 <sup>A</sup>	3.32 ± 1.07 <sup>A</sup>	0.98 ± 0.08 <sup>A</sup>	0.96 ± 0.001 <sup>A</sup>
2% salt	9.20 ± 1.04 <sup>B</sup>	2.25 ± 1.04 <sup>B</sup>	0.75 ± 0.05 <sup>B</sup>	0.87 ± 0.001 <sup>B</sup>
4% salt	4.77 ± 1.04 <sup>C</sup>	1.73 ± 1.05 <sup>C</sup>	0.46 ± 0.05 <sup>C</sup>	0.64 ± 0.001 <sup>C</sup>

Note. Means with different capital letter superscripts are significantly different from one another at  $P < 0.05$ .

<sup>a</sup> Units of plant mass are in grams. Values are back-transformed least square means of log<sub>e</sub>(total plant mass) and log<sub>e</sub>(root mass). The least square means of log<sub>e</sub>(root mass) are adjusted for the covariate log<sub>e</sub>(shoot mass). Back-transformed least square means of arcsine square root (bolting frequency).

<sup>b</sup> The root to shoot allometry is the slope of the regression of log<sub>e</sub>(root mass) on log<sub>e</sub>(shoot mass).



**Fig. 2** Population means ( $\pm$ SE) across all treatments of (a) total plant biomass, (b) root mass adjusted for shoot mass, and (c) bolting frequency in *Solidago sempervirens*. d, Percent reduction in total mass averaged across the 2% and 4% salt treatments relative to the no-salt treatment for each population. Plant-mass values are in grams and are back-transformed from least squares means of  $\log_e$  mass; values for bolting frequency are back-transformed from least squares means of arcsine-square root frequency. Black-filled symbols: coastal dune populations A and B; gray-filled and cross-hatched symbols: New England roadside populations; open symbols: Watkins Glen populations.

plants maintain large root biomass as a means of ensuring adequate water uptake in the face of increasing salinity. The lower allometric exponent of root mass to shoot mass with increasing salt might argue against the latter hypothesis.

Although all phenotypic traits of *S. sempervirens* varied among populations, only two traits, bolting frequency and salt tolerance (as measured by percentage reduction in total mass in salt treatments compared to the control), showed a geographic pattern of differentiation (fig. 2). The pattern was strong for bolting frequency and weaker for salt tolerance.

Two factors might favor differentiation in bolting (flowering) from west to east. The first concerns differential selection on reproductive allocation across habitats. Life-history theory predicts high reproductive allocation in habitats where adult mortality is high relative to juvenile mortality (Cole 1954). Higher reproductive effort would be advantageous in roadside habitats if they experience more frequent catastrophic disturbances than coastal dunes (but see Cartica and Quinn 1982; Lee 1993, 1995). Our observations indicated that coastal populations consisted mainly of established plants, with few seedlings present. In contrast, we noticed large numbers of seedlings at several of the roadside populations and also noted that several of these sites showed evidence of mowing and herbicide use, both of which might make roadsides very ephemeral environments. It is unclear, however, whether differences in population structure are the cause or effect of differences in reproductive allocation since we did not measure differences between sites in seed production and survival.

Geographic variation in selection on flowering time also could explain the observed differentiation in bolting frequency in *S. sempervirens* in the greenhouse. Recall that population variation in bolting frequency may reflect differences in the phenology of flowering rather than differences in reproductive allocation. In the wild, *S. sempervirens* flowers in the fall in

**Table 4**

**F-Tests for Preplanned Contrasts on Total Plant Mass, Root Mass Adjusted for Shoot Mass, and Bolting Frequency between Populations**

Contrast	Total plant mass		Root mass		Bolting frequency	
	df	F	df	F	df	F
Coastal vs. inland	1,155	27.14***	1,919	9.01**	1,154	487.97**
Coastal vs. inland 0% salt	1,380	2.08	1,932	2.15	1,449	119.50**
Coastal vs. inland 2% salt	1,375	7.17**	1,675	6.89**	1,449	262.88**
Coastal vs. inland 4% salt	1,375	58.25***	1,931	5.30*	1,449	246.92**
Coastal vs. roadside <sup>a</sup>	1,155	3.81	1,908	10.05**	1,154	319.98**
Coastal vs. roadside 0% salt <sup>a</sup>	1,380	0.81	1,930	3.22	1,448	86.86***
Coastal vs. roadside 2% salt <sup>a</sup>	1,375	0.06	1,710	4.37*	1,448	182.48**
Coastal vs. roadside 4% salt <sup>a</sup>	1,375	17.88***	1,931	5.33*	1,448	141.07**
Old vs. new <sup>b</sup>	1,150	2.33	1,832	4.41*	1,155	4.26*
Old vs. new 0% salt <sup>b</sup>	1,359	1.08	1,931	5.74*	1,450	0.01
Old vs. new 2% salt <sup>b</sup>	1,359	1.80	1,633	2.43	1,450	0.01
Old vs. new 4% salt <sup>b</sup>	1,359	1.17	1,152	0.27	1,450	15.84**

Note. Coastal = populations A, B; inland = populations C–I; roadside = populations C–E; old = population F; new = populations G–I.

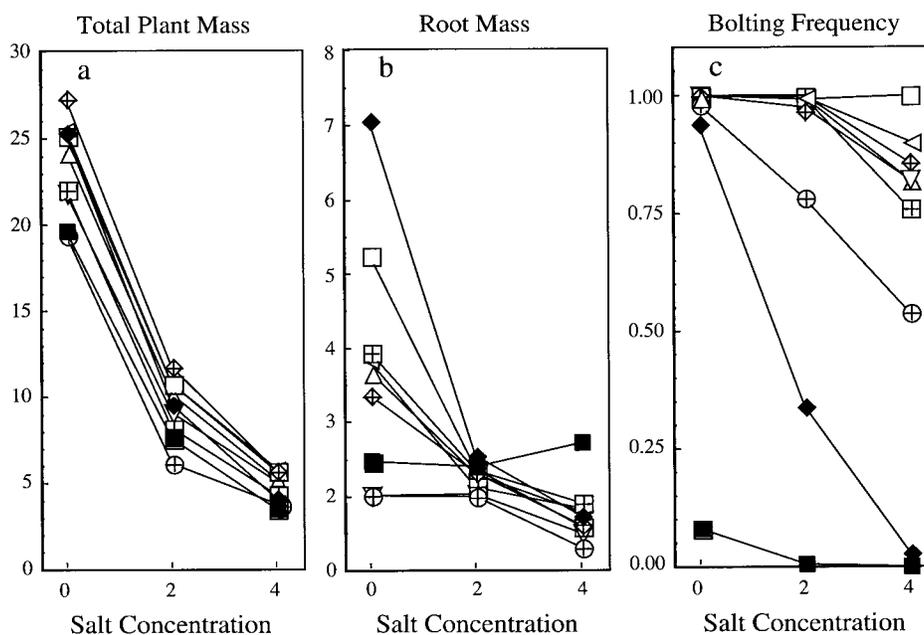
<sup>a</sup> Refers to New England populations.

<sup>b</sup> Refers to Watkins Glen populations.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.0001$ .



**Fig. 3** Means ( $\pm$ SE) of (a) total plant biomass (g), (b) root mass adjusted for shoot mass (g), and (c) bolting frequency in nine populations of *Solidago sempervirens* in the three salt treatments. Means are back-transformed as in fig. 2; symbols as in fig. 2.

response to short days (Goodwin 1941). Goodwin (1941, 1944) showed that coastal populations are genetically variable for flowering time, with northern (Massachusetts) populations flowering earlier than southern populations (Florida) when grown in a common garden. Earlier flowering also would be expected in inland habitats with a colder and more continental climate relative to eastern sites with milder, maritime climate. At the latitude of the nine *S. sempervirens* populations included in this study, the average number of frost-free days (a measure of growing season length) decreases from 247 d in Cape Cod, Mass. to 217 d in the area of Watkins Glen, N.Y. (<http://www.weatherbase.com>).

There was a slight increase in salt tolerance from eastern to western populations. Average as well as peak salt concentrations in soils (g NaCl/g soil) subject to deicing salts can be considerably higher than concentrations in dune sands (Hofstra and Smith 1984; Barbour et al. 1985). As a consequence, roadside populations might be selected for greater salt toler-

ance than coastal populations, and selection for tolerance would likely increase from west to east with increasing use of deicing salts in colder climates.

Population differentiation in association with environmental gradients provides strong circumstantial evidence of adaptation (Endler 1977), and, in the case of *S. sempervirens*, would provide evidence for the species' ability to modify its range distribution in response to novel environments. Definitive tests of adaptation in *S. sempervirens* with respect to reproductive traits and salt tolerance would require reciprocal transplant studies. We also cannot say whether population differentiation in *S. sempervirens* has occurred *in situ* or is the result of colonization from different seed sources.

While the strong effect of population on all phenotypic characters indicates genetic differentiation in phenotype, the degree of differentiation varied between populations. Populations from the area around Watkins Glen (F-I) were more similar to each other than to populations from the New England tran-

**Table 5**  
Estimates of Variance Components Attributable to and  $\chi^2$  Tests of Random Effects in Analyses of Total Plant Mass, Root Mass, and Bolting Frequency

Source	Total plant mass		Root mass		Bolting frequency	
	Variance	$\chi^2$	Variance	$\chi^2$	Variance	$\chi^2$
Block	0.0002	11.83	0.0000	1.82	0.0012	2.55
Block $\times$ treatment	0.0105	69.03***	0.0101	55.87***	0.0039	2.06
Block $\times$ population	0.000	0.00	0.0016	0.44	0.0136	10.69**
Family (population, block)	0.0137	57.96***	0.0057	11.38**	0.0052	0.52
Treatment $\times$ family (population, block)	0.0032	1.75	0.0079	5.43	...	...
Error	0.0432		0.0551		0.1182	

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.0001$ .

sect (A–G), and differentiation was greater among New England populations (fig. 2). These results are not surprising in that population divergence is expected to increase with the geographic distance between populations, with time since divergence, and as a function of the diversity of seed sources. The populations around Watkins Glen are much closer geographically than the other populations. Additionally, since the site is isolated, all populations in the area are most likely derived from one source population (F) and thus trace back to a recent common origin. In contrast, the New England populations are separated by greater distances and may have been colonized from separate seed sources.

There were significant family effects on trait values, confirming the existence of genetic variation for the phenotypes. However, we were unable to detect statistically significant genetic variance within most populations. Power analyses indicate that the latter result may be due to our small sample size of families (20 per population) and of progeny per family (two per family per treatment).

In conclusion, we have shown that populations across the expanding range of *S. sempervirens* are genetically different from coastal populations and from each other, and this di-

vergence is likely to have happened within the past 20–30 yr. For several traits (bolting frequency and salt tolerance), the differences between populations are suggestive of adaptation to different environments.

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