Impacts of salinity and simulated herbivory on survival and reproduction of the threatened Gulf of St. Lawrence Aster, *Symphyotrichum laurentianum*

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Abstract: Halophytic plants may experience joint, and potentially interacting, effects of salinity and herbivory on their survival and reproduction. We investigated the impacts of salinity and (simulated) herbivory on fitness in the Gulf of St. Lawrence Aster (*Symphyotrichum laurentianum* (Fernald) Nesom; Asteraceae). In natural populations, this species experiences varying soil salinity and spill-over herbivory from insects associated with neighbouring seaside goldenrod (*Solidago sempervirens* L.). We subjected *S. laurentianum* individuals to three levels of simulated herbivory (0%, 20%, and 40% leaf-area removal) and three levels of salinity (0, 10, and 20 g·L^{-1}) in three runs of a growth-chamber experiment. The effects of salinity and herbivory were always additive. Salinity consistently and strongly reduced survivorship, by as much as 80% at 20 g·L^{-1} salt, but significantly affected the seed set of survivors in only one run. Herbivory reduced survival significantly in one run (by 42% at 40% leaf-area removal) and reduced seed set of survivors (by 36% at 40% leaf-area removal) in another. While both stresses can have important effects on *S. laurentianum* fitness, the effects of salinity were more consistently strong than were the effects of herbivory, for both survival and seed set.

Key words: salinity, herbivory, halophyte, plant conservation, seed set.

Résumé : Les plantes halophytes peuvent subir les effets concomitants, et possiblement interactifs, de la salinité et de l'herbivorie sur leur survie et leur reproduction. Les auteurs ont examiné les impacts de la salinité et de l'herbivorie simulée sur l'adaptabilité de l'aster du golfe St-Laurent (*Symphyotrichum laurentianum*; Asteraceae). Les expériences conduites dans des populations naturelles de cette espèce consistaient à varier la salinité du sol et de l'herbivorie venant d'insectes associés à la verge d'or (*Solidago sempervirens*) voisine du bord de mer. Ils ont soumis des individus du *S laurentianum* à trois degrés d'herbivorie (0, 20 et 40 % d'élimination des feuilles) et trois degrés de salinité (0, 10 et 20 g·L^{-1}) dans une expérience répétée trois fois en chambre de croissance. Les effets de la salinité et de l'herbivorie s'additionnent toujours. La salinité réduit régulièrement et sévèrement la survie, atteignant 80 % avec 20 g·L^{-1} de sel, mais n'a affecté la mise à graine et la survie que dans une seule des répétitions. L'herbivorie a réduit significativement la survie dans une répétition (avec l'ablation de 42 % et 40 % du feuillage) et a réduit la mise à graine et la survie (avec l'ablation de 36 % et 40 % du feuillage) dans une autre. Alors que les deux stress peuvent exercer des effets importants sur l'adaptabilité du *S. lauretianum*, les effets de la salinité s'avèrent régulièrement plus néfastes que les effets de l'herbivorie, à la fois pour la survie et la mise à graine.

Mots-clés : salinité, herbivorie, halophyte, conservation des plantes, mise à graine.

Introduction

Both biotic and abiotic stresses can impact plant distributions and population sizes, and for plants of conservation concern, these stresses may make the difference between persistence and extirpation, locally or even regionally. Historically, for most plant systems, abiotic stresses have received greater emphasis than biotic ones (e.g., Ayres 1993; Campbell and Halama 1993; Moloney and Levin 1996; Pearson and Dawson 2003), with insect herbivory in particular largely assumed to be unimportant at the population level (Louda 2001). More recently, there is consensus that insect herbivory can sometimes have important effects on plant population dynamics (Halpern and Underwood 2006; Maron and Crone 2006), and while data are scarce, the potential importance of herbivory appears to extend to threatened and endangered plants (J. Ancheta and S. Heard, unpublished manuscript). Furthermore, abiotic stresses and biotic ones (including insect herbivory) sometimes interact in surprising and important ways (e.g., Bertness et al. 1987; Rand 2003; Schile and Mopper 2006; Eyles et al. 2009; Mody et al. 2009; Chaneton et al. 2010).

Abiotic stresses are particularly obvious in saline environments, where halophytic plant species endure physiological stress from salt exposure, but this is often coupled with considerable biotic stress from competitors and herbivores. The effects of biotic and abiotic stresses on halophyte fitness need not be additive (e.g., Bertness et al. 1987; Hemminga

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and van Soelen 1992; Ungar 1998; Rand 2003), and when stresses interact synergistically, populations may be particularly strongly impacted. Understanding the interplay of abiotic and biotic stresses will be critical in efforts to manage threatened and endangered halophytes, which are often under additional pressure from coastal development, irrigation, and other anthropogenic stresses (e.g., St. Omer and Barclay 2002; Patten et al. 2008; Lidón et al. 2009).

The Gulf of St. Lawrence Aster (*Symphyotrichum laurentianum* (Fernald) Nesom) (Asteraceae) is an excellent example of a species that may experience joint effects of salinity and herbivory stress in its native habitat. This rare annual halophyte, endemic to small areas of coastal Atlantic Canada, experiences reduced germination and seedling growth under high salinity (Houle et al. 2001), although the effects of salinity on post-seedling growth and reproduction have not been studied. It is also subject to spill-over herbivory, owing to its close spatial association with seaside goldenrod (*Solidago sempervirens* L.) (Asteraceae) (Jacques Whitford Environment Limited 1994; COSEWIC 2004). *Solidago* and *Symphyotrichum* both belong to the tribe Astereae, and the genera frequently share oligophagous insect herbivores (e.g., Herzig 1995; Goodwin and Fahrig 2002). Two insect herbivores in particular are common on *S. sempervirens* and have also been observed on *S. laurentianum*: a seed-predatory coleophorid moth, *Coleophora triplicis* McDunnough (Boudreau and Houle 1998; Steeves et al. 2008) and a folivorous chrysomelid beetle, *Trirhabda borealis* Blake (COSEWIC 2004). While seed predation on *S. laurentianum* (Steeves et al. 2008) has obvious fitness effects, since attacked seeds are directly killed, the effect of folivory has not been studied and its implications for plant fitness are less obvious. Plant mortality from folivory is unusual for established perennials (Crawley 1989) but possible for seedlings and annuals like *S. laurentianum* (Crawley 1989; Piqueras 1999; Norghauer et al. 2010), while reductions in seed set are a common consequence of folivory (Crawley 1989; Strauss and Zangerl 2002), especially for annuals.

The potential impacts of salinity and herbivory stress on survival and seed set of *S. laurentianum* are important because the species is an annual reproducing only by seed, with a rather limited soil seed bank (Stewart and Lacroix 2001; Kemp and Lacroix 2004). Recovery plans for *S. laurentianum* are currently being drafted (Matthew Wild, Canadian Wildlife Service, Montreal, Quebec, Canada; personal communication, 2010) and implemented (NB DNR 2007; Couillard and Jolicoeur 2008), with one conservation option being the establishment of new populations by explanting from greenhouse stocks. If folivory has an important impact on *S. laurentianum* fitness, and if folivory arises via spill-over from related plants, then site selection for explants should consider potential for spill-over herbivory as well as microsite salinity. Alternatively, for both explants and natural populations of *S. laurentianum*, potential local sources of spill-over herbivory (like populations of the non-threatened *S. sempervirens*) could be removed or treated with insecticide.

We assessed the effects of salt stress and simulated folivory on *S. laurentianum* survival and seed set in three runs of a growth-chamber experiment. We tested for salinity and folivory main effects and their interaction, using levels of each stressor that may plausibly be experienced by natural populations or by future explants.

Materials and methods

Study species

Symphyotrichum laurentianum is a rare annual halophyte endemic to coastal salt marshes, dune slacks, and similar habitats in Prince Edward Island, New Brunswick, and the Magdalen Islands of Quebec. Soils at *S. laurentianum* sites are typically very sandy. Plants are generally gynomonoecious, with female or hermaphrodite florets (Lacroix et al. 2007), flowering in August and September. *Symphyotrichum laurentianum* is self-compatible, with estimates derived from population genetics suggesting a modest amount ($\sim 16\%$) of outcrossing (Heard et al. 2009). The species reproduces only by seed, and because it does not appear to have significant potential for resource storage, seed production is likely to depend strongly on resource acquisition and photosynthesis in summer and early autumn.

Symphyotrichum laurentianum is listed as "threatened" under Canada's Species at Risk Act, but since this designation it has experienced population declines across its range (NB DNR 2007; Steeves et al. 2008; Heard et al. 2009) with many local populations much reduced or extirpated. Outside the Magdalen Islands, in 2009 the distribution of the species had been reduced to one population in each of PEI and NB (Paul Ayles, Parks Canada, PEI National Park, Charlottetown, Prince Edward Island, and Lewnanny Richardson, Piper Project, Rivière à la Truite, New Brunswick; personal communications, 2009).

Among the abundant neighbours of *S. laurentianum* is seaside goldenrod (*Solidago sempervirens*, Asteraceae), which often supports populations of at least two insect herbivores that can also attack *S. laurentianum*. The folivorous beetle *Trirhabda borealis* (Chrysomelidae) can cause extensive defoliation of *S. sempervirens* in close proximity to *S. laurentianum* populations (J. Ancheta, unpublished data) and has been observed on *S. laurentianum* (COSEWIC 2004), although without any assessment of its impact. The seed-predatory moth *Coleophora triplicis* (Coleophoridae) is common on *S. sempervirens*, and has caused extensive damage (>50% seed predation) to *S. laurentianum* in at least one year in one Prince Edward Island (PEI) population (Steeves et al. 2008). While the impact of seed predators on the fitness of *S. laurentianum* is obvious, the indirect effects of leaf-area loss from folivory have not been studied for this species.

The extent to which *S. laurentianum* is exposed to salinity may vary considerably among microhabitats and across its range. In PEI sites, salinity may be moderated by inputs from the fresh water table (Wells and Hirvonen 1988). At least some *S. laurentianum* sites in PEI, experience soil–water salinity as low as 1–8 g·L^{-1} (Kerry-Lynn Atkinson, Dept. of Biology, University of Prince Edward Island, Charlottetown, PEI, personal communication, 2009), but standing water in typical *S. laurentianum* habitats may be 11–31 g·L^{-1} (Giberson et al. 2001; DFO 2007). Furthermore, *S. laurentianum* will certainly experience salinity up to 31 g·L^{-1}, at least temporarily, via seawater inundation during tidal flooding and storm surges. Houle et al. (2001) reported

that salinity levels above 15 g·L^{-1} strongly inhibited *S. laurentianum* seed germination, but impacts of salinity on post-germination growth and reproduction have not been well studied.

Experimental methods

We conducted three replicate runs of an experiment assessing the impact of salinity and simulated herbivory on the survival and reproduction of *S. laurentianum*. Each time, we manipulated soil salinity and simulated herbivory (leaf-area removal) in a 3 × 3 factorial design, measuring plant survival and lifetime fitness through production of mature (filled) seed. At the University of New Brunswick (UNB), Fredericton, we worked with plants from a greenhouse population that was itself derived from a greenhouse population at the University of Prince Edward Island (Heard et al. 2009). The original seed source was a natural population of *S. laurentianum* within Prince Edward Island National Park; this population, at Blooming Point East Marsh, is no longer extant (Heard et al. 2009).

We germinated seeds, recently harvested from greenhouse-grown plants, in 9 cm diameter Petri plates lined with two pieces of filter paper (9 cm medium porosity, VWR, West Chester, Pennsylvania, USA) soaked in deionized water. We placed the plates in a growth cabinet (16 h (day) at 25 °C – 8 h (night) at 20 °C) for approximately 3 weeks. Seedlings were then transplanted to 10 cm square pots filled with Pro-Mix BX^{TM} potting mixture (Premier Tech, Rivière-du-Loup, Que.) in 15 cm diameter plastic saucers. Pro-Mix differs from soils at typical *S. laurentianum* sites in having much more organic material and less sand. Potted plants were held for the duration of each run in a controlled environment chamber (Conviron Inc., Winnipeg, Manitoba, Canada), under a light regimen which started on a 16 h (day) at 25 °C – 8 h (night) at 20 °C schedule (daytime light intensity ∼60 μmol·m^{-1}·sec^{-1}) at constant 80% relative humidity. We shortened the daylight period by 30 min·week^{-1} until we had reached a 9 h day and 15 h night. In our first two runs we implemented the daylight reduction beginning with an adjustment of 2 h after 4 weeks, followed by 30 min adjustments each week; in the third run, we made 60 min adjustments every second week from the beginning of the run.

We used three levels of salinity (0, 10, or 20 g·L^{-1}) and three levels of simulated herbivory via leaf-area removal (0%, 20%, and 40%) for a total of nine treatments. Plants were exposed to these treatments over a growth period of approximately 3 months, until nearly all plants had either flowered or died.

Our salinity levels should span the range of salinity commonly experienced by *S. laurentianum* in the field, including the East Marsh population from which our greenhouse population was originally founded. However, they do not capture the highest levels to which plants are probably exposed for short periods during events like storm surges. We watered twice per week from both the bottom and top of the pots, and either watered until saucers overflowed or dumped excess water from the saucers to avoid buildup of salt in the soil beyond intended levels. Salt water at the appropriate salinity was produced by dissolving Instant Ocean^{TM} aquarium salt (Spectrum Brands, Atlanta, Georgia, USA) in deionized water.

Simulated herbivory was inflicted by clipping every leaf on a plant, as it expanded, with a single-hole paper punch to give the intended fraction of leaf area removal. To quantify leaf area removal and ensure that we could apply damage consistently to leaves across the natural size range, we photocopied a set of *S. laurentianum* leaves to cardstock for use as templates. We included nine leaves in each of three size classes (large, >5 cm length; medium, 2–5 cm; and small, <2 cm). These cardstock leaf images were then cut out and weighed, and then clipped with a paper punch until 20% or 40% of their weight had been removed. The resulting clipped "leaves" served as visual templates for the amount of damage to be inflicted on the experimental plants. These levels of clipping bracketed observed levels of folivory on natural populations of *Solidago sempervirens* neighbouring *S. laurentianum* in PEI (J. Ancheta, unpublished data). Such *S. sempervirens* populations exist within 20 m of most known *S. laurentianum* populations, including the East Marsh population from which our greenhouse population was founded. Unfortunately, the literature includes reports of folivore presence on *S. laurentianum*, but no estimates of damage. Our own surveys showed negligible damage to *S. laurentianum* in one population in one year (Prince Edward Island National Park, PEI; J. Ancheta, unpublished data), but substantial temporal and spatial variation in herbivore damage are extremely common in nature. We therefore based our clipping levels on damage to *S. sempervirens* populations from which spillover herbivores are likely to arise, and view them as representing potential rather than known damage levels for *S. laurentianum*.

Our first replicate run (December 2007 to March 2008) had 38 plants per treatment (342 plants total), run 2 (December 2008 to February 2009) had 28 plants per treatment (252 total), and run 3 (November 2009 to February 2010) had 19 plants per treatment (171 total). We reduced the number of plants per treatment for logistical reasons, although reduced germination also contributed to the size of run 3. At the end of each run, we scored plants for survival, collected seedheads from each surviving plant, and dissected them to count achenes (an achene is the single-seeded fruit of each floret in Asteraceae). Achenes were categorized as filled or unfilled, with filled achenes being conspicuously larger and darker. We refer to the number of filled achenes in all capitula of an individual as that individual's "seed set". Unfilled achenes do not contain viable seed and are excluded from our analyses; we did not attempt to distinguish between unfertilized ovules, fertilized but aborted seeds, and fertilized but unfilled seeds. We did not consider pollen export as a fitness component, because in greenhouse and growth chamber experiments pollen export is expected only to extend to other florets in the same capitulum (Heard et al. 2009); thus, seed set provides an integrated measure of both male- and female-function fitness.

Statistical analyses

We performed all statistical analyses using SAS (version 8.0; SAS Institute Inc., Cary, North Carolina, USA). To examine the effects of salt, herbivory, run, and their interac-

Table 1. Log-linear analysis of survivorship as a function of salinity and herbivory.

	Source	df	χ^2	P	Effect size*
Run 1	Salt	2	19.1	<0.0001	–43%
	Herbivory	2	3.44	0.18	–19%
Run 2	Salt	2	15.1	0.0005	–36%
	Herbivory	2	1.65	0.43	+7%
Run 3	Salt	2	42.3	<0.0001	–80%
	Herbivory	2	11.6	0.0030	–42%

*Effect size is the percentage change in percent survivorship from the control to the higher treatment level (20 g·L^{-1} salt or 40% herbivory).

tions on *S. laurentianum* survivorship, we used log-linear analysis in PROC CATMOD. To examine the effects of salt, herbivory, run, and their interactions on seed set of surviving plants, we used ANOVA in PROC GLM, reporting tests based on Type III sums of squares. Some residuals deviated significantly but moderately from normality, but since ANOVA is generally robust to violations of normality for balanced designs (Khan and Rayner 2003) we consider our parametric results reliable.

We began each analysis with a single 3-way model analyzing data from all three runs, but after finding significant treatment × run interactions we conducted and report separate log-linear analyses and ANOVAs for each run. In these separate analyses, we began with models considering salt, herbivory, and their interaction, but since the interaction terms never neared significance, we pooled them with the error term before reporting tests of main effects. Retention of the interaction terms would not change the interpretation of any of our results.

We estimated effect sizes for each factor in each run. Each effect-size estimate for salinity is based on mean survivorship or seed set at zero salinity, taken as the sample-size-weighted mean across herbivory levels, compared with mean survivorship or seed set at 20 g·L^{-1} salinity. For herbivory, the analogous calculations use the 0% and 40% herbivory treatments and weighted averages across levels of the salinity treatment; in both cases, the effect is expressed as a percentage change from the control level of survivorship or seed set.

Results

Survivorship

The effects of salinity and herbivory on *S. laurentianum* survivorship varied among runs (salinity × run, $\chi^2_{(4)}$ = 15.0, P = 0.0048; herbivory × run, $\chi^2_{(4)}$ = 11.60, P = 0.021; three-way log-linear analysis). In separate analyses of survivorship for each run, the salinity × herbivory interaction never approached significance (all $\chi^2_{(5)}$ ≤ 5.0, P ≥ 0.29). Although the effect size varied, exposure to high salinity caused strong and significant reductions in individual survivorship in each run (Table 1; Fig. 1), reducing survivorship by up to 80% at 20 g·L^{-1} and up to 60% at 10 g·L^{-1}. Simulated herbivory significantly reduced survivorship in run 3 (by 42% at 40% leaf-area removal; Table 1; Fig. 1). There was a more modest and non-significant trend towards reduced survival at high leaf-area removal in run 1, but no trend in run 2.

Fig. 1. Impacts of salinity and simulated herbivory on survivorship of *S. laurentianum*. Plots display means plus or minus 95% confidence intervals calculated from the binomial distribution.
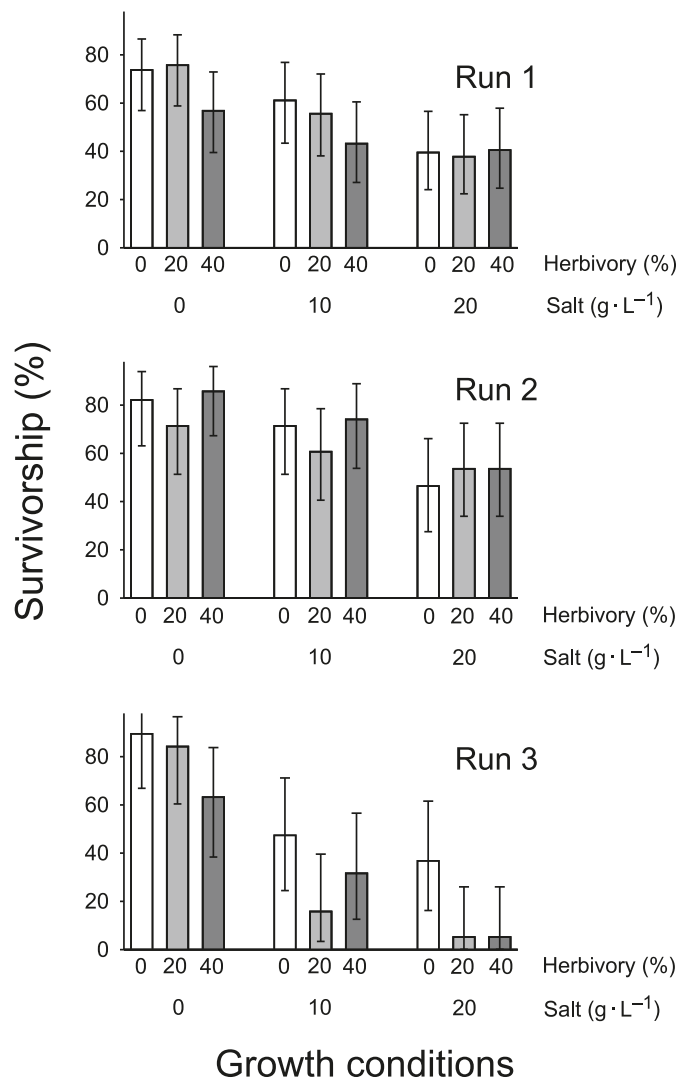
Seed set

The effect of salinity, but not herbivory, on seed set of surviving *S. laurentianum* varied among runs (salinity × run $F_{[4,391]}$ = 11.3, P < 0.0001; herbivory × run $F_{[4,391]}$ = 0.68, P = 0.61; three-way mixed-model ANOVA). In separate analyses of seed set for each run, the salinity × herbivory interaction never approached significance (all $F_{[4,170]/[4,158]/[4,63]}$ ≤ 1.14, P ≥ 0.34). We detected significant

Table 2. ANOVA analysis of seed set (of surviving plants) as a function of salinity and herbivory.

	Source	df	MS	F	P	Effect size*
Run 1	Salt	2	32200	24.2	<0.0001	–90%
	Herbivory	2	4170	3.13	0.046	–36%
	Error	174	1330			
Run 2	Salt	2	321	1.93	0.15	–38%
	Herbivory	2	325	1.95	0.15	–41%
	Error	162	167			
Run 3	Salt	2	10.5	0.12	0.89	—[†]
	Herbivory	2	129	1.48	0.24	—[†]
	Error	67	87.5			

*Effect size is the percentage change in seed set from the control to the higher treatment level (20 g·L^{-1} salt or 40% herbivory), estimated using least square means.

[†]Reliable effect size estimates are not available because too few plants survived to set seed.

impacts of both salinity and herbivory in run 1 (Table 2; Fig. 2), with the effect of salinity especially striking (90% reduction at 20 g·L^{-1}) although the herbivory effect was far from negligible (36% reduction at 40% leaf area removal). In run 2, we observed similar trends (Fig. 2), but seed set was much lower overall and neither treatment effect was significant (Table 2); in run 3, seed set was lower still, and because few plants survived at high salinity or high herbivory, we could not make reliable estimates of effect sizes.

Discussion

Our data do not support the hypothesis of interactions (either synergistic or compensatory) between salinity and herbivory for *S. laurentianum*, with all salt × herbivory interactions far from significant (Tables 1, 2). Instead, we saw additive effects of herbivory and salinity. Both salinity and herbivory had major impacts on *S. laurentianum* fitness (in at least one run) even at our intermediate treatment levels. Salinity reduced survivorship, for instance, by up to 60% at 10 g·L^{-1} salt and by up to 80% at 20 g·L^{-1}, while in the one run where it had a significant effect, herbivory reduced survivorship by 39% and 42% at leaf-area removal of 20% and 40%. Note that because we grew our plants in ProMix, which has considerably higher organic matter content than soils at typical *S. laurentianum* sites, we expect that our estimate of the impact of salinity is a conservative one (soil organic matter tends to mitigate effects of soil salinity; e.g., Tejada et al. 2006).

While there was considerable variation among runs in effect sizes, overall we found stronger effects of salinity than of herbivory (at the levels tested, which were designed to mimic levels plausible in nature). We speculate that the systemic nature of salt exposure may impact fitness more severely than leaf-area removal, which leaves behind reduced but healthy photosynthetic tissue. We also found more consistently strong effects on plant survivorship than on seed set of survivors. We detected significant effects on seed set only in run 1 (Table 2), which may reflect at least in part differences in statistical power; we used fewer plants in runs 2 and 3, and seed set is defined only for the subset of those plants that survived.

The considerable variation in effect sizes among runs of our experiment (with significant run × salinity and run × herbivory interactions) surprised us, given that the bulk of

Fig. 2. Impacts of salinity and simulated herbivory on seed set of surviving *S. laurentianum*. Note changes in vertical axis scale among runs. Plots display means plus or minus two standard errors (approximate 95% confidence intervals).
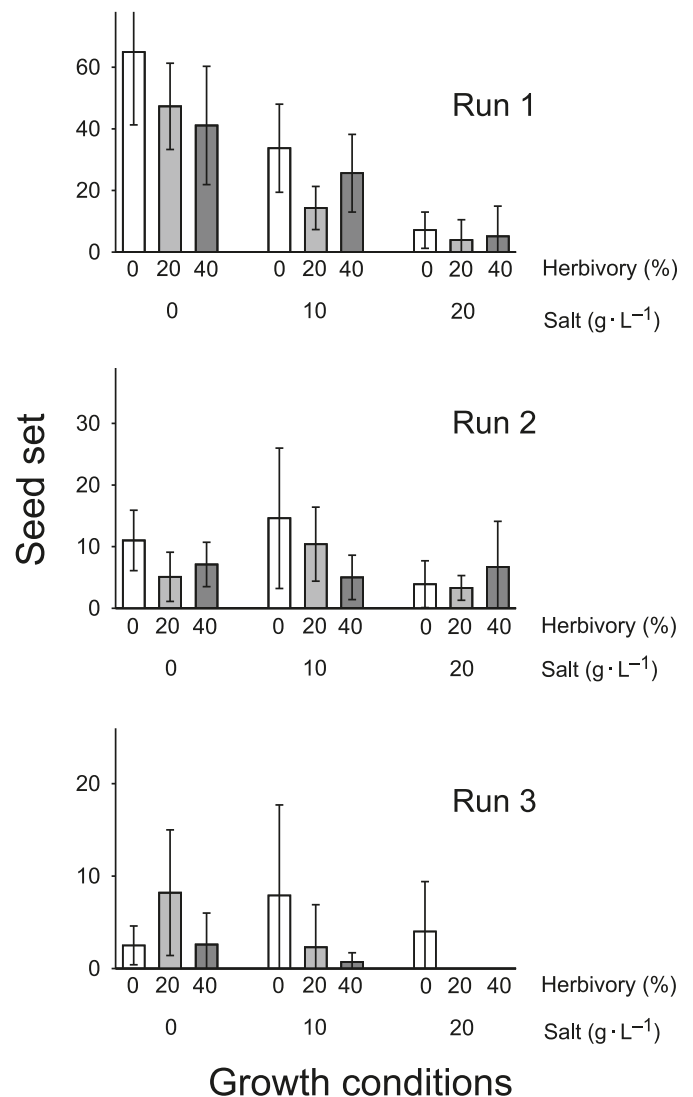
our experiment was run under growth-chamber conditions with controlled light, temperature, and humidity. We suspect that conditions during germination and transplanting, which were less comprehensively controlled across runs, may have interacted with our treatments. Interactive effects of salinity and other environmental variables on plant growth have been observed in other systems (e.g., Ehret et al. 1990; El-Keblawy and Al-Rawai 2005; Redondo et al. 2004; Al-Khateeb 2006). The slightly different photoperiod regime in run 3 could, at least in principle, also have interacted with our treatments. For seed set (but not survival), another possibility is differences in pollination among runs. We did not deliberately pollinate flowers in our experimental populations. Seed set exceeded 20% of floret number (the typical fraction of hermaphroditic florets) for many plants in our first run, but seldom in runs 2 and 3. Therefore, in run 1, female-only florets set seed in addition to hermaphroditic florets, and this suggests that jostling by plant handling or air ventilation were enough to promote pollination at least among florets within capitula. With fewer plants in later runs, wider spacing and reduced handling may have led to reduced pollination, constraining seed set and thus limiting the scope for effects of salinity and herbivory. Whatever the full explanation for the run × treatment effects we observed, if salinity and herbivory interact with such seemingly minor details of husbandry, it may be challenging to predict the effects of these stressors on *S. laurentianum* fitness in the field.

There is controversy over the use of artificial clipping treatments to simulate the effects of real herbivory (e.g., Karban and Myers 1989; Baldwin 1990; Hjältén 2004; Agrawal 2005). While the effects of clipping often differ from the effects of natural herbivore attack, differences between clipping and natural herbivory are much less frequent for studies of growth and reproduction (vs. induced resistance and other physiological variables) and much less frequent for studies of invertebrate (vs. vertebrate) herbivory (Lehtilä and Boalt 2004). In our system, therefore, clipping should be relatively realistic as a simulation of herbivore damage. Furthermore, clipping offers the possibility of damage levels that are experimentally controlled and consistent across experiments.

Folivores are not the only guild of insect herbivores that might be important in natural *S. laurentianum* populations. In particular, a severe impact of the seed-predatory moth *Coleophora triplicis* (54% seed predation) was documented for one PEI population in 2004 by Steeves et al. (2008). However, the population dynamics of *Coleophora* (and thus its potential impact on *S. laurentianum*) are highly variable both in space and time: Steeves et al. (2008) reported negligible attack in a second *S. laurentianum* population only 400 m away, and 3 years later, we found only 7% seed predation (J. Ancheta, unpublished data) in the population where Steeves et al. (2008) reported 54% predation. It is difficult to compare the potential impacts of seed predators and folivores on *S. laurentianum* because for both guilds, data on natural attack rates are sparse and strong spatiotemporal variation is expected. However, we imposed levels of folivory that are common on related and neighbouring *S. sempervirens*, and were such levels of folivory to occur on *S. laurentianum* as well our data (run 1; Tables 1 and 2) suggest effects on reproductive output at least as severe as

the 54% loss to seed predation documented by Steeves et al. (2008).

Our results have important implications for *S. laurentianum* management. The recently published New Brunswick recovery plan for *S. laurentianum* did not recommend explants because factors that limit *S. laurentianum* populations were insufficiently understood (NB DNR 2007), while the Quebec recovery plan (Couillard and Jolicoeur 2008) and a national recovery plan under development recognize explants as a potentially valuable tool for preventing local extirpations and founding new populations. When the site selection process must weigh potential impacts of different stressors at different sites, our results highlight salinity as a more consistently important stressor for *S. laurentianum* than potential folivory. Nevertheless, the threat of herbivory (both folivory and seed predation) via spill-over from the related goldenrod, *S. sempervirens*, is real, and the potential loss of seed production from herbivory is far from negligible. Managers may want to choose explant sites away from *S. sempervirens* (provided that this does not incur a cost of increased salinity). Alternatively, managers could avoid herbivore export from *S. sempervirens* by local removal of the plants or (to control *Coleophora*) their seedheads, ideally at a time when herbivore individuals would be removed along with their hosts. Insecticide treatment could also be a management option, albeit with a need to consider its significant potential for non-target effects.

Acknowledgements

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