

Synergistic and additive effects of drought stress and simulated herbivory on two goldenrods, *Solidago altissima* and *S. gigantea*

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Abstract: Understanding the combined effects of stressors on plants is important for understanding how they will tolerate herbivory and other damage under unfavorable conditions. When two stresses have synergistic effects, plants may experience particularly strong impacts. We examined individual and combined effects of drought stress and clipping (simulated herbivory) on two species of goldenrods (*Solidago altissima* L. and *S. gigantea* Ait.). Each stress reduced production of most plant structures, with drought stress having stronger impacts than clipping. The effects of the two stresses were additive for *S. gigantea* but synergistic for *S. altissima*, at least for aboveground biomass and inflorescence biomass. Both species, when under stress, reallocated resources toward asexual reproduction (rhizomes) and away from sexual reproduction (inflorescences). Our results suggest that even closely related plants may tolerate damage differently when under abiotic stresses, and that predicting the additive vs. synergistic action of combined stresses will be difficult.

Key words: drought, herbivory, clipping, stress, resource allocation.

Résumé : Il est important de comprendre les effets combinés d'agents stresseurs sur les plantes afin de comprendre comment elles toléreront l'herbivorisme et d'autres dommages en conditions défavorables. Lorsque deux stress ont des effets synergiques, les plantes peuvent subir des impacts particulièrement importants. Nous avons examiné les effets individuels et combinés d'un stress hydrique et du pincement (simulant l'herbivorisme) sur deux espèces de verge d'or (*Solidago altissima* L. et *S. gigantea* Ait.). Chaque stress réduisait la production de la plupart des structures végétales, la sécheresse ayant des impacts plus forts que le pincement. Les effets des deux stress étaient additifs chez *S. gigantea* mais synergiques chez *S. altissima*, au moins quant à la biomasse hors-sol et la biomasse de l'inflorescence. Les deux espèces, lorsque soumises à un stress, réalloyaient leurs ressources vers la reproduction asexuée (rhizomes) et s'éloignaient de la reproduction sexuée (inflorescences). Les résultats des auteurs suggèrent que même des plantes étroitement reliées peuvent tolérer des dommages de manière différente en condition de stress abiotique, et que de prédire l'action additive ou synergique de stress combinés sera difficile. [Traduit par la Rédaction]

Mots-clés : sécheresse, herbivorisme, pincement, stress, allocation des ressources.

Introduction

In natural environments, plants are commonly exposed to multiple stresses that can compromise their fitness. Both biotic and abiotic stresses can reduce growth, reproduction, and survivorship of many plant species (e.g., Calow 1989; Jones and Jones 1989). Under extreme conditions, such as drought, salinity, or extensive herbivory, a plant's physiological functions and defense pathways may become disrupted (e.g., Smirnoff 1998; Serrano et al. 1999), leading to severe fitness declines and even death.

Studies of biotic or abiotic impacts on plants often focus on one stress at a time (e.g., Lotze and Worm 2002;

Collins and Smith 2006). However, under natural conditions, plants often endure abiotic and biotic stresses in combination. If the combined impact of two stresses is equal to the sum of the impacts of each stress alone (additive stresses), studies focusing on single stresses are not misleading (Bansal et al. 2013). However, in other cases two stresses might be interactive, with combined impact less than or greater than the sum of the separate impacts. When stresses interact, studying them independently cannot predict their joint impact. This is perhaps most important with respect to the possibility of greater-than-additive impacts (synergy). Synergistic impacts are plausible because damage from one stress may compro-

Received 1 March 2016. Accepted 4 May 2016.

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mise physiological or other responses to a second stress, and the result of such synergy may be particularly strong impacts on plant populations (Trumble et al. 1993; Rand 2003).

Nearly all plant species experience some stress from herbivory. When other stresses act as well, plant responses to herbivory may be altered, with complex and perhaps unpredictable consequences for plant performance (Trumble et al. 1993; Paez et al. 1995; Bansal et al. 2013). When herbivory and abiotic stresses interact synergistically, the result may be serious negative impacts on plant individuals and populations (Chapin et al. 1987; Rand 2003; Eyles et al. 2009). Of particular interest for many plants is the potential for interaction between herbivory and drought stress (Marquis 1992; Hawkes and Sullivan 2001; Holmgren et al. 2006). With increasing global temperatures, drought conditions are becoming more common (Ayres and Lombardero 2000; Schär et al. 2004), bringing increased potential for synergistic impacts if drought stress decreases plant tolerance of herbivore damage (Hawkes and Sullivan 2001; Levine and Paige 2004; Vinebrooke et al. 2004; Williams and Jackson 2007; Wise and Abrahamson 2007; Atala and Gianoli 2009).

Assessing responses to a given stress can be complicated by the fact that not all plant tissues or organs need to respond identically. In fact, plants may respond to stress by reallocating resources among plant structures, such as aboveground and belowground tissues (e.g., Ackerson and Hebert 1981; Oosterheld and McNaughton 1991; March et al. 2013). As a result of such reallocation, stress may trigger changes in a plant's life history, such as shifts between sexual and asexual reproduction.

We asked whether drought stress and clipping (to simulate herbivory) have synergistic or additive effects on two species of goldenrod: *Solidago altissima* L. and *S. gigantea* Ait. (Asteraceae). These species both experience frequent herbivory and periodic episodes of drought. These closely related and ecologically similar species are a widely used model system for studies of plant–insect interactions (e.g., Abrahamson and Weis 1997; Heard and Kitts 2012; Williams and Avakian 2015), plant invasions (e.g., Sakata et al. 2015; Szymura and Szymura 2016), life history evolution (e.g., Schmid et al. 1995; Hafdahl and Craig 2014), and other issues in evolutionary ecology. We examined the impact of drought stress and early-season clipping on different plant structures (both aboveground and belowground) and on patterns of resource allocation among them. Surprisingly, we found synergistic interactions between the stresses for one species, but not for the other.

Materials and methods

Study system

Solidago altissima and *S. gigantea* are perennial plants of prairies and disturbed habitats (such as old fields

and roadsides), and are abundant and frequently syntopic across much of eastern and central North America (Abrahamson and Weis 1997). Both species occur in clonal patches. Asexual reproduction occurs in early spring, when new shoots (ramets) arise from overwintered rhizomes (generally quite short in *S. altissima*, but up to 30 cm long in *S. gigantea*). Sexual reproduction involves the copious production of wind-dispersed achenes in early fall. These goldenrods are hosts to many generalist and specialist insect herbivores and may experience a variety of herbivore and environmental stresses.

Experimental design

In May 2014, we haphazardly collected 51 *S. altissima* and 97 *S. gigantea* rhizomes from an old field in Fredericton, New Brunswick (45°57'N, 66°37'W). We collected rhizomes at least one metre apart to reduce the likelihood of collecting plants of the same genotype. Rhizomes were returned to the greenhouse and fragments ~7–15 cm were immediately planted in Pro-Mix BX potting mix (Premier Tech, Riviere-du-Loup, Quebec, Canada) in 13 cm × 13 cm × 15 cm pots. We fertilized the pots with a 14-14-14 (nitrogen–phosphorous–potassium) slow releasing fertilizer (Nutricote; 5 mL per pot) and randomized them to bench positions. For each species, once a quarter of the plants had reached 25 cm in height (range ~10–30 cm), we randomly assigned plants to four treatment groups in a clipping × drought stress factorial design. Clipping involved removing one quarter of a plants' main shoot with pruning shears. Such damage resembles browsing herbivory and is also in many ways attack by stem-galling insects (especially the gelechiid moth *Gnorimoschema gallaesolidaginis*, which damages or destroys apical meristems; Heard and Kitts 2012). Although the impacts on plants of natural herbivory and artificial clipping are not identical, differences tend to be small in studies dealing with plant growth and reproduction (Lehtila and Boalt 2004). We monitored plants daily, and watered “no drought stress” plants whenever their soil became dry. Drought-stressed plants were not watered until they started to wilt, at which point we supplied just enough water for them to regain turgor pressure. This type of pulsed drought is representative of natural drought stress in many systems (Huberty and Denno 2004). We chose a water-when-wilted method rather than setting absolute rates of water supply because the amount of water required to avoid drought stress will depend on plant size and architecture, weather (sun and temperature), position on the greenhouse bench, and many other factors. That is, we controlled the amount of drought stress plants experienced rather than the amount of water they received.

Data collection

On day 83 after planting, most plants showed signs of senescence, and we collected them by clipping the stems at the soil level and storing the aboveground parts in

zip-lock bags in a refrigerator. Pots, still containing belowground tissues in soil, were stored (moist but without further watering) in a cold room for about 4 weeks, after which we harvested belowground tissues by washing soil with high pressure water through a screen. We separated belowground tissue into two components: roots and rhizomes, storing them in zip-lock bags pending drying and weighing. A few individuals of *S. altissima* produced no rhizomes at all (with no hint that this might depend on treatment), and a very few samples were degraded during storage before weighing; we ignored these in corresponding analyses. We separated aboveground tissue into three components: leaves, stems, and inflorescences (including in the latter not just flowers but phyllaries, receptacles, peduncles, and associated tissues). We dried each component separately for 48 h at 60 °C before weighing them to the nearest 0.01 g.

Statistical analysis

We assessed the impact of drought stress and clipping on total aboveground biomass by comparing treatment groups (fixed effects) with a two-way ANOVA for each species. We conducted similar analyses for inflorescence, rhizome, and root biomasses. We log-transformed biomass data to stabilize variances, and also because biomass effects are likely to be multiplicative. For inflorescence biomass, we included in the ANOVA only those plants that flowered, and we analyzed impacts of treatments on likelihood of flowering separately using a general linear model (GLM) with a binomial error distribution.

Results

Impacts on plant parts

Clipping plants and imposing drought stress reduced the biomass of most plant components, as expected (the full dataset is available in the Supplementary data, Table S1¹). For most components, drought effects were stronger than clipping ones. However, the two species differed in the occurrence of synergistic interactions between stresses.

For *S. gigantea*, drought stress led to significant reductions in percent flowering and in all tissue components, whereas clipping reduced flowering and all components except rhizomes (Table 1; Figs. 1a–1e). The effects of stress were large: for example, drought reduced aboveground biomass by more than half (from 20.1 g for controls to 8.1 g for drought-stressed plants), and clipping by almost a third (from 20.1 to 13.7 g; Fig. 1a). There was no suggestion of synergy between the two stresses for any variable (all clipping × drought stress interactions far from significance; Table 1).

Table 1. Analyses of impacts from clipping (“clip”) and drought-stress (“drought”) on *Solidago gigantea*.

Factor	df	MS/SE ^a	F/Z ^b	P
Aboveground biomass				
Clip	1	1.68	7.97	0.006
Drought	1	17.2	81.7	<0.001
Clip × drought	1	0.435	2.07	0.15
Residuals	93	0.210		
Percent flowering				
Clip	—	8.93	2.76	0.006
Drought	—	12.64	2.00	0.045
Clip × drought	—	3.02	0.00	0.91
Inflorescence biomass				
Clip	1	8.83	8.13	0.006
Drought	1	12.6	11.5	0.001
Clip × drought	1	3.02	2.75	0.10
Residuals	54	1.10		
Rhizome biomass				
Clip	1	0.04	0.11	0.75
Drought	1	7.08	18.6	<0.001
Clip × drought	1	0.14	0.36	0.55
Residuals	86	0.38		
Root biomass				
Clip	1	2.37	7.33	0.008
Drought	1	26.6	82.3	<0.001
Clip × drought	1	0.22	0.68	0.41
Residuals	86	0.32		

Note: All analyses are two-way ANOVA, except percent flowering, which is a general linear model.

^aFor percent flowering, entry is the standard error.

^bFor percent flowering, entry is the Z-value.

For *S. altissima*, drought stress led to significant reductions in aboveground biomass, inflorescence mass, and root mass (Table 2, Figs. 2a, 2c, and 2e). A parallel trend toward reduced likelihood of flowering (Fig. 2b) was not significant. Clipping reduced the likelihood of flowering and all tissue components except rhizomes (Table 2; Figs. 2a–2e; although the apparent effect on root mass only approached significance). As for *S. gigantea*, stress treatments led to strong effects: for example, drought stress reduced aboveground biomass by about 40% (13.7 to 8.4 g; Fig. 2a). However, *S. altissima* differed from *S. gigantea* in that the two stresses acted synergistically, at least for aboveground and inflorescence biomasses (significant clipping × drought stress interactions; Figs. 2a and 2c; Table 2). The effect of this interaction on plant biomass was substantial. For example, clipping did not reduce final size for well-watered plants (with clipped plants actually a bit larger, 14.2 vs. 13.7 g), but it reduced the size of drought-stressed ones by half (8.4 to 4.2 g; Fig. 2a). This pattern was even stronger for inflorescence biomass (Fig. 2c). Percent flowering and root biomass showed similar patterns (Figs. 2b and 2e), but these interactions were not statistically significant.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjb-2016-0060>.

Fig. 1. Patterns in biomass, flowering, and tissue allocation in *Solidago gigantea* plants under drought and clipping stress. Box plots for aboveground (a), inflorescence (c), rhizome (d), and root (e) biomass show means (dots), medians (lines), 25th/75th percentiles (boxes), and 10th/90th percentiles (whiskers), all after \log_{10} transformation. Fraction flowering (b) shows mean and 95% confidence intervals from the binomial distribution. Tissue allocation (f) shows fraction of total biomass made up of rhizomes, roots, stems, leaves, and inflorescence.

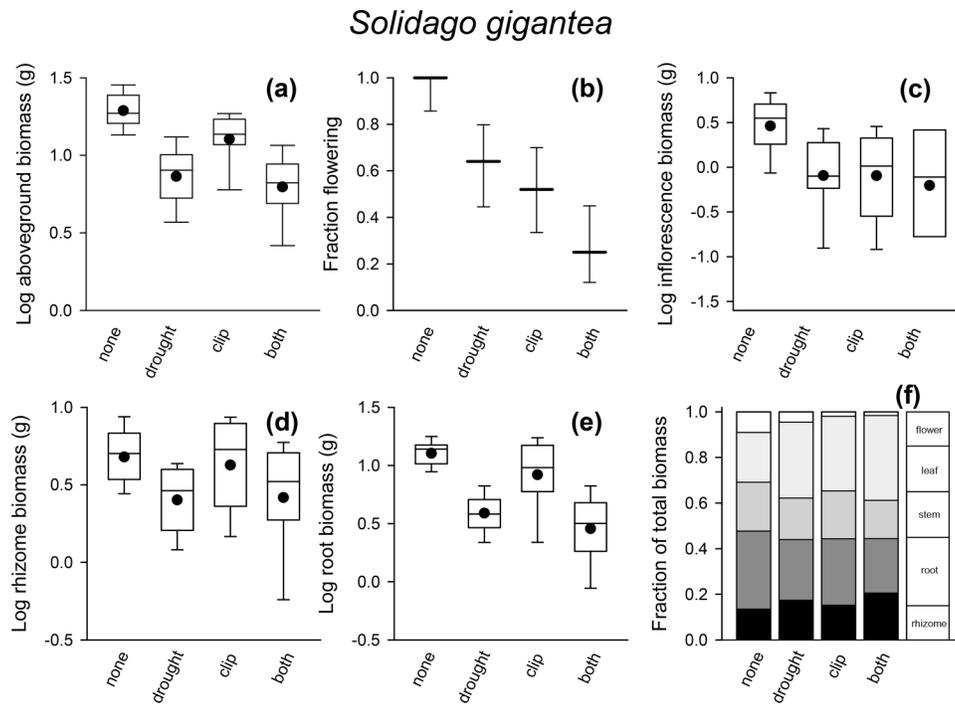


Table 2. Analyses of the impacts of clipping (“clip”) and drought-stress (“drought”) on *Solidago altissima*.

Factor	df	MS/SE ^a	F/Z ^b	P
Aboveground biomass				
Clip	1	2.24	8.06	0.007
Drought	1	9.64	34.6	<0.001
Clip × drought	1	1.68	6.02	0.018
Residuals	47	0.278		
Percent flowering				
Clip	—	1.01	2.87	0.004
Drought	—	0.876	1.10	0.27
Clip × drought	—	1.40	-0.62	0.54
Inflorescence biomass				
Clip	1	12.8	10.8	0.003
Drought	1	12.6	10.7	0.003
Clip × drought	1	14.3	12.1	0.002
Residuals	25	1.18		
Rhizome biomass				
Clip	1	2.58	2.64	0.11
Drought	1	0.19	0.20	0.66
Clip × drought	1	0.30	0.31	0.58
Residuals	35	0.98		
Root biomass				
Clip	1	2.33	3.46	0.069
Drought	1	8.70	12.9	<0.001
Clip × drought	1	1.10	1.64	0.21
Residuals	35	0.98		

Note: All analyses are by two-way ANOVA, except percent flowering, which is a general linear model.

^aFor percent flowering, entry is the standard error.

^bFor percent flowering, entry is the Z-value.

Impacts on patterns of allocation

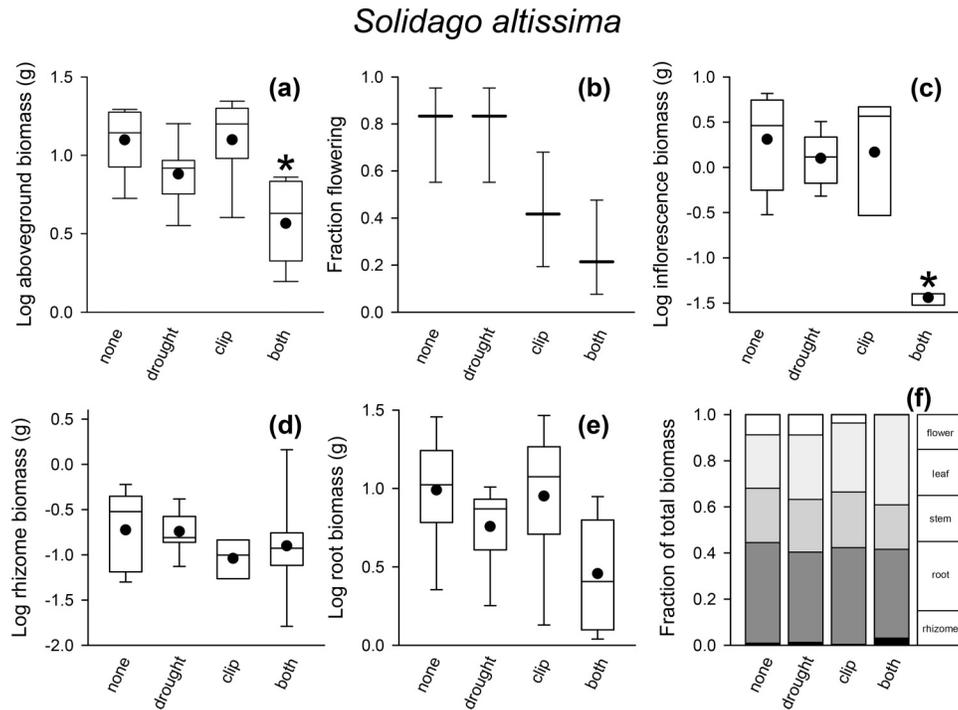
In addition to assessing effects on tissue components individually, we visualized patterns of allocation by dividing total plant biomass among components. While there is some variability among treatments in allocation to all components, the overall trend is that stresses result in allocation away from inflorescences and toward rhizomes (compare top and bottom compartments in the stacked bars; Figs. 1f and 2f).

Discussion

Drought stress and clipping reduced biomass of most tissue components in both of our goldenrod species. This, of course, is not surprising. What is more interesting is that drought stress and clipping acted synergistically in *S. altissima* (at least for aboveground and inflorescence biomasses), but not for *S. gigantea*. Furthermore, responses to individual and combined stresses influenced resource reallocation across different plant structures. As a consequence, stressed plants underwent major shifts in life history strategies, including most notably reallocation of resources from sexual to asexual reproduction.

We measured aboveground biomass because many studies in plant population and community ecology focus on this variable (e.g., Grime 1989; Ancheta et al. 2010; Bansal et al. 2013). This is partly because aboveground biomass is straightforward to measure in the field, but also because it is likely to be an important fitness corre-

Fig. 2. Patterns in biomass, flowering, and tissue allocation in *Solidago altissima* plants under drought and clipping stress. All panels and plotting conventions as in Fig. 1. Asterisks in panels (a) and (c) indicate statistically significant interaction between effects of the two stresses.



late because it scales with photosynthetic surface area (Patterson and Flint 1980; Jones and Jones 1989), and thus with energy acquisition to support growth, physiology, and reproduction. Both clipping and drought stress reduced the biomass of several plant components, although when each acted alone, drought stress had by far the greater effect, which suggests considerable plant tolerance to (simulated) herbivory. For *S. altissima* (but not for *S. gigantea*), the two stresses acting together were synergistic: well-watered plants were almost completely tolerant of clipping, but drought-stressed plants were not.

We were surprised by the occurrence of synergy in one species but not the other, because *S. altissima* and *S. gigantea* are closely related, ecologically very similar, and often grow syntopically. They do have quite different cuticle properties (*S. gigantea* having a glabrous and extremely waxy stem, whereas *S. altissima*'s stem is pubescent; there are similar leaf-surface differences). This could certainly lead to differences in cuticle permeability, which modulates water loss under drought-stressed conditions (Schönherr 1982; Riederer and Schreiber 2001; Goodwin and Jenks 2007). One might speculate that plants suffering more from drought stress might be more impacted by herbivory, perhaps synergistically, as a consequence. However, because we watered our drought-stressed plants only at wilting, we would expect our two goldenrod species to have been suffering equally, even if it took lower soil moisture to reach the wilting point for one than the other. Without additional experiments studying plant-physiological consequences

of manipulations like ours, it is difficult to ascribe the differing drought stress \times clipping interactions to cuticular differences or other functional mechanisms.

The synergistic effect of drought stress and clipping suggests greater vulnerability of *S. altissima* populations to stress, especially under the increasing frequency of drought conditions expected in many models of global climate change. This may not be of direct conservation concern, given that *S. altissima* is widespread, abundant, and generally considered widespread, abundant, and easily spreading. Effects on *S. altissima*, however, may drive drought effects on the composition of plant communities, and thus (indirectly) on other community members. Furthermore, that synergistic action can exist for *S. altissima* makes it a plausible concern for other species too. Perhaps most importantly, the difference in outcome for our two study species suggests that it will not be a simple matter to predict when, or for which species, multiple stressors will act additively and when they will act synergistically.

Belowground tissues were more tolerant than aboveground ones to damage from single or combined stresses. Rhizomes, in particular, were nearly unaffected by either stress (the only significant effect being a modest one of drought stress on *S. gigantea*). Note that rhizome allocation is much lower in *S. altissima* than in *S. gigantea*, regardless of treatment, because of the former species' much shorter rhizomes. Root biomass was reduced modestly by clipping (with the effect not quite significant for *S. altissima*), although there was a stronger

effect of drought stress, with reduction in each species of 50% or more. We were surprised by this reduction: one might expect drought stress to drive increased root production instead, as plants work to tap into difficult-to-reach water sources (Fenner 1983; Blum 1996; Gianoli and González-Teuber 2005). However, not all plant species increase their root mass when drought-stressed (Schulze 1986; Grace 1997), and it is possible that allocation of limited resources to reproductive and photosynthetic structures brings greater fitness returns under natural drought conditions.

As a consequence of the stresses we imposed (singly or in combination), there was a shift in allocation from sexual to asexual reproduction. Resources were invested in maintaining rhizome biomass, while fewer plants flowered at all, and for those that did flower, inflorescence biomass was greatly reduced. In the clipping treatments, one might imagine failure to flower being just a consequence of our removal of the apical meristem (although damaged goldenrods do often flower from released lateral meristems). However, meristem damage cannot account for reduced flowering in drought-stressed treatments. Inflorescence production is correlated with plant size in many species, and many plants may have a minimum size that allows them to flower (e.g., Weiner 1988; Schmid et al. 1995). Our stress treatments may well have reduced plant size below such a threshold.

It is commonplace for environmental stresses to influence resource allocation and to affect trade-offs between two reproductive modes (e.g., Van Zandt et al. 2003; Pluess and Stöcklin 2005). In many cases clonal plants increase sexual reproduction and decrease asexual reproduction when stressed, presumably because stress suggests a mismatch between genotype and environment and thus favours offspring genetically different from the parent (Van Zandt et al. 2003). Our goldenrods, though, showed the opposite shift, which may be because resource availability considerations act in opposition to genetic-variation ones. This tension would exist if the minimum-size threshold for inflorescence production is lower than the corresponding threshold for asexual reproduction (e.g., Pluess and Stöcklin 2005). We suspect that severely stressed *Solidago* plants are simply too small to reproduce well sexually (perhaps because the effectiveness of floral displays in attracting pollinators often increases nonlinearly with display size; de Jong and Klinkhamer 2005), but are large enough to produce rhizomes (which do not suffer from the same non-linearity). Another possibility is that under stressful conditions, there is no certainty that produced seed will establish (Prati and Schmid 2000). It might be adaptive, then, for plants to invest more resources into rhizomes, which are already belowground and more buffered from stresses than seed or young seedlings. Furthermore, in *Solidago* (as in many plant species; e.g., Hutchings 1987; Mehrhoff 1989), rhizomes will stay dormant until the

following season, allowing growth when conditions may be more favourable. Resolving these alternative explanations for *Solidago*'s reallocation under stress would require data on the fate of rhizomes and seeds under differing but realistic field conditions. This is a challenging prospect for a plant that produces seed in tiny achenes with long-distance dispersal by wind.

Our very simple experiment revealed complex responses to stress in *S. altissima* and *S. gigantea*, and important differences in stress response between these close and ecologically similar relatives. As global climate changes, bringing environmental conditions to which plant populations are not adapted, understanding such responses will be increasingly important, but our data suggest this will not be a simple matter. Our *Solidago* species may be valuable model systems for future attempts to tease apart traits involved in tolerance to herbivory, drought, and other stressors.

Acknowledgements

We are grateful to Matt Methven, Bethany Nordstrom, and Mischa Giasson for assistance in the greenhouse, field, and lab, and to Laurie Yeates for access to root-washing equipment at the Canadian Forest Service. Discussion with Steve Hendrix throughout the project improved our experimental design and interpretation, while Les Cwynar, Linley Jesson, Rob Johns, Dave MacLean, and two anonymous reviewers made helpful comments on the manuscript. Our work was supported by Discovery Grants to S.B.H. from the Natural Sciences and Engineering Research Council of Canada.

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