Impact of attack by *Gnorimoschema* gallmakers on their ancestral and novel *Solidago* hosts

Stephen B. Heard · Emily K. Kitts

Abstract Interactions between insect herbivores and host plants can involve herbivore-host pairs that are evolutionarily ancient or only recently associated. Novel herbivore-host species pairs are continually being formed via host shifts, dispersal, and increasingly via anthropogenic introductions. Conceptual models of enemy-victim coevolution (specifically, the evolution of plant tolerance and of insect virulence) suggest that the impact of an herbivore on its novel host should, at least at first, be more intense than its impact on its ancestral host. We tested this hypothesis for the specialist gallmaking caterpillar *Gnorimoschema gallaesolidaginis* (Lepidoptera: Gelechiidae) on its ancestral and novel hosts, *Solidago altissima* and *S. gigantea*. We measured aboveground ramet mass for paired attacked and unattacked ramets of each species at two sites (Fredericton, NB, and Toronto, ON, Canada), and also measured allocation of tissue mass to stems, leaves, and flowers in galled and ungalled ramets. *G. gallaesolidaginis* attack reduced ramet growth considerably more on *S. gigantea*, the novel host, consistent with the coevolutionary hypothesis. We were unable to detect reallocation of tissues in galled ramets as a mechanism for tolerance, and found no intraspecific difference in the impact of gallmaking on allocation patterns. Herbivore host shifts between alternative native hosts will provide an excellent opportunity to understand the evolutionary history of novel herbivore-host associations, particularly (as in the *Solidago* system) when multiple insect herbivores have host-shifted across the same plant pair.

Keywords Evolution of tolerance · Evolution of virulence · Herbivory · Host shift · Herbivore impact · Plant-insect interactions

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Introduction

Associations between insect herbivores and their host plants (like those between other kinds of natural enemies and victims) can be dynamic in both space and time. While some enemy-victim pairs coevolve in pairwise fashion for long periods, many and perhaps most will reshuffle their associations in time and/or space. Both herbivore host range and a plant's herbivore fauna can vary geographically (Thompson 2005; Logarzo et al. 2011), and herbivore-host associations change through evolutionary time via host-range evolution (Dres and Mallet 2002; Diegisser et al. 2009; Kato et al. 2010), the assembly or evolution of novel communities during climate change (Stastny et al. 2006; Pena and Wahlberg 2008; Winkler et al. 2009), or large-scale dispersal events (Bertheau et al. 2010). With the increasing prevalence of anthropogenic effects on biotas, novel associations also form frequently as exotic species interact with members of their new communities (Graves and Shapiro 2003; Singer et al. 2008). Therefore, the formation of an evolutionarily novel herbivore-host association must always have been a frequent event, and is perhaps now more frequent than ever. We might expect such novel associations to differ from older ones in many ways, such as in the ecology of herbivore diet specialization and host-finding, plant resistance to attack, and the physiological and functional interplay of insect attack with plant defences.

The impact of herbivory on fitness of attacked plants could also differ between novel and ancestral associations, and if such differences exist, they could influence the course of plant-herbivore coevolution and shape plant–insect community structure. For example, patterns in herbivore impact will determine the relative strengths of selection arising from herbivory on the two hosts. Such patterns could also alter the relative abundance of co-occurring ancestral and novel hosts, and influence the distribution of herbivore diversity and abundance among hosts (e.g., Fornoni 2011). If impacts are stronger in novel associations, insect host shifts and introductions could be critical plant-conservation concerns (Heard and Ancheta 2011), whereas if impacts tend to be stronger in old associations then we might expect greater temporal turnover in community dominance as older hosts are suppressed but newer ones escape impact.

Should we expect greater or lesser impact of a given herbivore on a novel host plant (vs. the same insect on an ancestral host)? Once an herbivore has overcome plant resistance to mount a successful attack, its impact on the attacked plant will be determined by the interplay of insect virulence and plant tolerance. Insect virulence[1] reflects the kind and amount of damage inflicted by the herbivore during attack, and determines the level of damage sustained by the plant for a given herbivore load. Tolerance is the degree to which the plant is able to achieve fitness, through continued growth and reproduction, despite that damage (Strauss and Agrawal 1999). Conceptual models of enemy-victim coevolution (Pimentel 1963; Levin et al. 1982; Ewald 1994) suggest that novel associations are likely to pass through an evolutionarily transient phase during which the impact of herbivory is greater on the novel host. This prediction involves expectations for evolutionary changes in both insect virulence and plant tolerance. Changes in resistance can also occur, but are not directly relevant to questions about herbivore impact once resistance has been overcome.

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[1] In the insect-plant interactions literature, the word "virulence" is used in two very different senses. It can mean the ability of an insect to overcome plant defences (to overcome resistance), or it can mean the damage inflicted on the plant during the insect's attack (Wilhoit and Gould 1992). We are concerned here with the latter sense.

Natural enemies in general may evolve either decreased or increased virulence, depending on the net result of changing virulence for transmission between victims (Ewald 1994; Alizon et al. 2009). For insect herbivores on novel hosts we would expect selection to favour decreased virulence in most cases. Since attacking insects usually depend on the continued availability of plant resources (especially for herbivores such as gallmakers and leafminers that have persistent interactions with an individual host), they should be under selection to reduce the impact of their development on the plant (their virulence; e.g., Pimentel 1963; Levin et al. 1982). This pressure could be opposed if higher virulence improved the chances of herbivore transmission to new hosts (Ewald 1994). However, few if any of the factors that are known to link high virulence to enhanced transmission apply often to insect herbivores. For instance, high virulence can be favoured by vector or predator transmission between mobile hosts, when host-killing enhances release of infective enemies, when multiple enemy strains compete to reproduce within a host individual, when the enemy can complete its development regardless of host death, when enemies can survive for a long time in the absence of a host, or when enemies can move easily and cheaply between victims during a single generation (e.g. Ewald 1994; Levin and Bull 1994; Nowak and May 1994; Mosquera and Adler 1998; Messenger et al. 1999; Vigneux et al. 2008; Alizon et al. 2009). While some very mobile herbivores (such as grasshoppers) might have the last property, for most insect herbivores none of these situations will apply. Transmission efficiency of most insect herbivores will therefore not depend on high virulence, and so selection should favour reduced virulence (Levin and Pimentel 1981) for most herbivores.

Selection on tolerance is conceptually simpler: selection should generally favour increasing tolerance of attack, unless tolerance is very costly (Roy and Kirchner 2000). Costs of tolerance have been demonstrated for some plants, but seem small or absent for others (e.g. Núñez-Farfán et al. 2007; Hakes and Cronin 2011). Furthermore, when ancestral and novel hosts are closely related, we would expect similar costs of tolerance in the two hosts and thus selection in the novel host for increasing tolerance (since we expect plants to be relatively intolerant of unfamiliar attackers). Herbivores should therefore be better tolerated by plants with which they share a long history (e.g., Pimentel 1963; Hokkanen and Pimentel 1989; Agrawal 2011; Fornoni 2011), although the rate at which tolerance increases may be constrained by the possibility that tolerance trades off with resistance (Núñez-Farfán et al. 2007; Fornoni 2011).

Selection on virulence and tolerance should thus act in concert to reduce herbivore impact in evolutionarily old plant–insect associations, compared with novel associations in which selection has not yet had time to act. Both the virulence and tolerance arguments are stronger for specialist herbivores than generalist ones, and strongest for herbivores that do not move often between individual hosts, and therefore we would predict the largest novel-ancestral contrast in impact for internally feeding and sessile herbivores with narrow host ranges.

How do these theoretical expectations fare when confronted with data from real plant-herbivore interactions? The vast majority of relevant data comes from the exotic-species literature. New herbivore-host pairs are generated either as exotic plants come under attack by native (to the newly adopted range) herbivores, or as exotic herbivores begin to attack native plants. In a large meta-analysis of interactions between native and exotic herbivores and plants, Parker et al. (2006) found that evolutionarily novel herbivore-host interactions display more intense suppression of host by herbivore: exotic plants tend to be suppressed more strongly by (generalist) native insects than are native plants, and native plants are suppressed more strongly by exotic insects. However, Parker et al. (2006) did not separate

differences in plant resistance (whether exotic plants were attacked more often) from tolerance (differences in herbivore impact given attack). While there are high-profile examples of low tolerance to exotic herbivores (e.g., cedar scale, Hokkanen and Pimentel 1989; emerald ash borer, Rebek et al. 2008), as a whole the literature specifically examining plant tolerance shows a variety of patterns (Chun et al. 2010; Fornoni 2011), with tolerance of native herbivores low for some exotic plants but high for others. Furthermore, increased tolerance may evolve very quickly during some invasions (Huang et al. 2010; Fornoni 2011). On balance, then, data from the exotic-species literature are consistent with, but do not unambiguously support, greater impact in evolutionarily novel interactions.

While studies of exotic plants and herbivores provide useful windows on the evolutionary ecology of novel herbivore-host pairs, inference from exotic-native systems has several limitations. First, the evolutionary novelty of the exotic-native interaction is always confounded with a major geographical shift for one of the two species, such that in addition to a new herbivore (or host), the plant host (or herbivore) is simultaneously adapting to new climate, competitors, pathogens, and so on. Second, few exotic-native pairs are yet very old, with the vast majority dating back no more than a century or two. While there is evidence for evolutionary changes in novel herbivore-host interactions even over a few decades (e.g. Carroll et al. 1997; 2005; Abhilasha and Joshi 2009; Huang et al. 2010), we can infer little from this about the expected pace and outcome of evolution over longer time scales. Third, many novel host-herbivore associations in the exotic-species literature involve oligophagous or polyphagous herbivores; indeed, the enemy-escape hypothesis for the success of invasions emphasizes release from attack when exotic plants leave behind the specialist herbivores that suppress them in their native range (Maron and Vila 2001). For more narrowly specialist herbivores, which are more likely to coevolve tightly with their hosts and thus show strong differences in impact between ancestral and novel hosts, the exotic-species literature has less to say.

A complementary opportunity to test hypotheses about novel herbivore-host pairs is offered by cases of recent host shifts between pairs of native plants. Such host shifts are common in phytophagous insects (Percy et al. 2004; Matsubayashi et al. 2010) and may or may not be followed by host-associated differentiation yielding pairs of host-specialist races or sibling species (Stireman et al. 2005). Surprisingly, despite an ever-increasing number of detailed studies of host-shifting phytophagous insects (e.g. Abrahamson and Weis 1997; Feder et al. 1998; Nosil 2007; Ferrari et al. 2008), we are aware of no data available to test the hypothesis that a recent host-shifter should have a greater impact on growth and/or reproduction of its evolutionarily novel host. We provide the first such test, for the host-specialist spindle-gall moth *Gnorimoschema gallaesolidaginis*. We predicted that *G. gallaesolidaginis* would have a greater impact on its novel host *Solidago gigantea* than on its ancestral host *S. altissima*.

Methods

Study species

The goldenrods *Solidago altissima* L. and *S. gigantea* Ait., two closely related members of the *Solidago canadensis* complex, share a diverse herbivore fauna (Maddox and Root 1990; Root and Cappuccino 1992; Fontes et al. 1994). *S. altissima* and *S. gigantea* are abundant and frequently syntopic in prairies, old fields and disturbed habitats across much of temperate North America (Semple and Cook 2006). They are long-lived rhizomatous

perennials, with new ramets growing from overwintered rhizomes each spring, flowering in late summer to fall, and senescing to ground level in late fall. Ramets export a substantial fraction of their photosynthate to the rhizomes to support asexual production of daughter ramets in the following year (Schmid et al. 1988b).

Among the host-specialist herbivores of *S. altissima* and *S. gigantea* is the gallmaker *Gnorimoschema gallaesolidaginis* (Riley) (Lepidoptera: Gelechiidae), which occurs from Nova Scotia to Alberta and south to Florida through New Mexico (Miller 2000; S.B. Heard, unpubl. data.). *G. gallaesolidaginis* has undergone a host shift from *S. altissima* to *S. gigantea* and has subsequently undergone host-associated differentiation on the two hosts (Stireman et al. 2005). The two host forms, with strict host fidelity and substantial reproductive isolation (allozyme $F_{ST} = 0.16$, $\sim 1.9\%$ mtDNA divergence; Nason et al. 2002; Stireman et al. 2005), are best described as either very well-differentiated host races or very young sibling species. The host shift likely took place at least 300,000 years ago (Stireman et al. 2005). *Gnorimoschema* larvae on the two *Solidago* hosts experience differences in plant-chemistry (Abrahamson and Weis 1997) and in natural enemy attack (Heard et al. 2006).

G. gallaesolidaginis is univoltine, with females mating and laying eggs in autumn (Leiby 1922; Miller 2000). Eggs overwinter among dead foliage or on the ground and hatch in spring; a first-instar caterpillar wanders to a newly emergent goldenrod shoot, initiates feeding among terminal leaves, and then burrows down the stem to initiate a hollow gall within which the larva feeds. Larvae pupate in late summer. Attack rates by *Gnorimoschema* larvae increase with shoot size on each host, with a similar strength of size dependence (at least in most years; Heard and Cox 2009). It is unknown whether this attack-rate pattern arises because of larval preference for large shoots or higher success initiating galls on larger shoots. Once initiated, galls are extremely persistent and are easily identified late in the growing season even if the gallmaker or galled shoot does not survive.

Collection and sample processing

We collected *Gnorimoschema*-galled and ungalled goldenrods from two sites where the two *Solidago* hosts grew in dense mixed stands: Fredericton, New Brunswick (45° 58′ N, 66° 39′ W), and Toronto, Ontario (43° 39′ N, 79° 23′ W). The Fredericton collections were made 28 Aug-1 Sept 2003 along walking trails 0–2 km north of the pedestrian bridge across the Saint John River, and the Toronto collections were made 15 Sept 2003 in an open field at the base of the Leslie St. Spit in Tommy Thompson Park.

Because we are not able to experimentally manipulate *G. gallaesolidaginis* attack in the field, we took a paired-observational approach to the assessment of patterns in gallmaker impact. At each site, we ran haphazardly-oriented belt transects (~ 50 cm wide at Fredericton, and ~ 1 m wide at Toronto) through dense patches of *Solidago* spp. In these transects we collected individuals of *S. altissima* or *S. gigantea* galled by *G. gallaesolidaginis* by cutting their stems at ground level (belowground parts were not collected). We did not collect galled ramets if they were extensively damaged by other herbivores, or by other agents (e.g., mammalian browsing). For each galled individual collected, we also collected the nearest ungalled neighbour of the same species—except that when an ungalled nearest neighbour had extensive herbivore or other damage, we rejected it and took the next nearest ungalled neighbour instead. We collected approximately 80 pairs of plants for each species at each site. Our paired design ensures that spatial variation in plant growth is not confounded with gallmaker attack.

We stored collected plants in Ziploc bags at −20°C until they could be processed. We separated each plant into three (ungalled plants) or five (galled plants) components: flowers (flower heads, including phyllaries, peduncles, and associated tissues; but referred to here as "flowers" for simplicity), leaves, stem, gall (if present), and gall equivalent (if galled). "Gall equivalent" was a section of stem directly below and equal in length to the gall, and was used to estimate the likely mass of the stem section that the gall replaced (because estimated stem mass should exclude the abnormal gall tissue but include the normal stem tissue from which the gall proliferated). We weighed each component after drying at 55–65° C for a minimum of 48 h. For galled stems, we added twice the mass of the gall-equivalent stem to that of the remaining stem to estimate total stem mass. We added stem, leaf, and flower mass to get total ramet mass. For galled stems, total ramet mass excludes the mass of the gall (although it includes an estimate of the normal stem the gall replaced), as we consider this mass lost to normal plant production.

Statistical analysis

Our data have a paired structure, with each galled ramet compared with its nearest ungalled neighbour. We calculated the difference in total ramet mass between galled and ungalled neighbours, and we call this quantity the "galled-ungalled mass difference", or "GUMD". (Expressing this as a percentage of average ramet size does not change our results or interpretation, so we present only the simpler analysis). For two randomly chosen ramets, such a difference would have an expected mean of zero. However, because *G. gallae-solidaginis* caterpillars disproportionately attack larger ramets of each host (Heard and Cox 2009), there is no simple expectation for the GUMD in our data. If the gallmaker had no impact on plant growth, we would expect larger ramet mass for galled ramets, and thus a positive GUMD, with any actual impact of gallmaker attack reducing or even reversing this pattern. Fortunately, the ramet-size effect on attack is of similar strength for both hosts (Heard and Cox 2009), and so if the GUMD is larger for one host than the other we can infer a difference between hosts in gallmaker impact. We also calculated the parallel contrast for flower mass, the galled-ungalled flower difference (GUFD), to test whether gallmaker impact on fitness via sexual reproduction differed between species. We were unable to assess impact on fitness via asexual reproduction because we did not collect underground rhizomes, although decreases in aboveground biomass are likely to correlate with reductions in rhizome production because of limitations to photosynthate supply (Schmid et al. 1988a).

We examined patterns in GUMD and GUFD using 2-way ANOVAs with species and sites treated as fixed factors. We treated 'site' as fixed because we were not interested in estimating variation among all possible sites. We also used paired t-tests to compare galled and ungalled ramets for each species and site, although we stress that because of gallmaker preference for larger shoots these comparisons are not simply interpretable as measures of gallmaker impact.

We calculated fractional allocation to stem, leaf and flower production for each ramet (stem, leaf and flower mass, respectively, divided by total ramet mass). These allocations are of interest because a ramet under herbivore attack will suffer a reduction in overall resources but might achieve increased tolerance by reallocating resources to reproductive structures. We calculated the galled-ungalled difference in leaf and flower allocations: galled-ungalled leaf allocation difference (GULAD) and galled-ungalled flower allocation difference (GUFAD). Because the three allocations are constrained to add to one, we do

not analyze patterns in stem allocation. We used 2-way ANOVAs to compare allocation differences across species and sites.

We conducted all statistical analyses in R (R Development Core Team 2010).

Results

For the ancestral host, *Solidago altissima*, galled ramets were larger than ungalled ones at both sites, although in paired t tests the difference was not significant at either site (Fig. 1a; Toronto $t_{(80)} = 1.79$, $P = 0.076$; Fredericton $t_{(60)} = 0.15$, $P = 0.88$). However, for the novel host, *S. gigantea*, galled ramets were significantly smaller than ungalled ones at both sites (Toronto $t_{(79)} = -2.20$, $P = 0.031$; Fredericton $t_{(74)} = -4.32$, $P < 0.0001$. This pattern is reflected in the galled-ungalled mass difference (GUMD), which differs strongly and significantly between species but not sites in 2-way ANOVA (Table 1a). Thus,
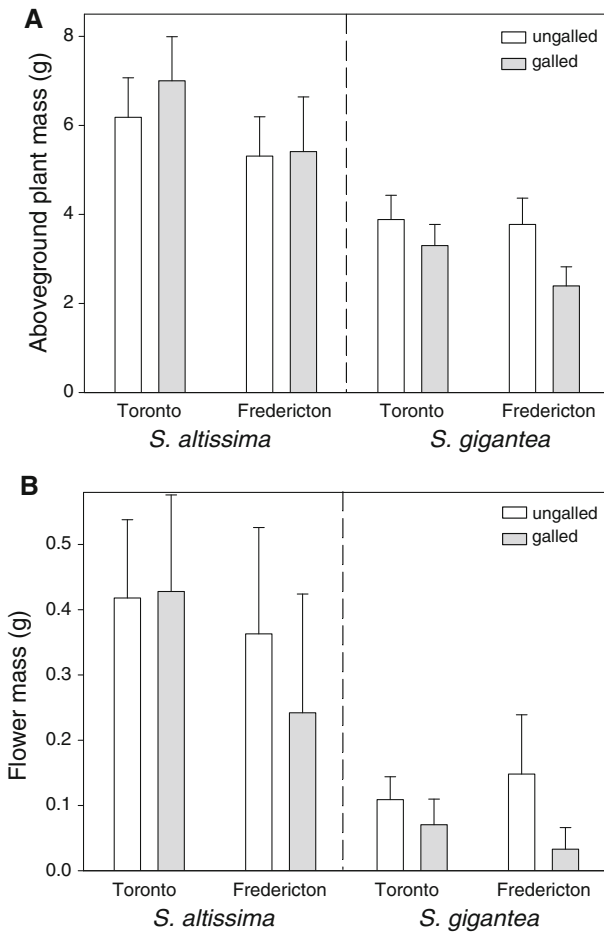

Fig. 1 Total aboveground dry mass (**a**) and flower dry mass (**b**) for galled and ungalled *S. altissima* and *S. gigantea*, at study sites in Toronto and Fredericton

Table 1 Analysis of (a) galled-ungalled mass difference (GUMD) and (b) galled-ungalled flower difference (GUFD) for *S. altissima* and *S. gigantea* at Toronto and Fredericton

	df	MS	F	P
(a) GUMD (difference in aboveground ramet mass)				
Host species	1	163	12.2	**0.00055**
Site	1	42.6	3.19	0.075
Species*site	1	0.105	0.008	0.93
Residual	293	13.4		

	df	MS[a]	F	P
(b) GUFD (difference in flower mass)				
Host species	1	64.0	0.181	0.67
Site	1	771	2.19	0.14
Species*site	1	54.6	0.155	0.69
Residual	293	352		

[a] Entry is MS $\times 10^3$

G. gallaesolidaginis has a much larger impact on overall plant growth for the novel host than for the ancestral one.

The pattern in flower production (which correlates with fitness through sexual reproduction; Lehnertz 1999) is largely parallel to the pattern in overall mass, but with much larger variation among ramets (Fig. 1, compare panels a and b). Galled ramets produced fewer flowers than ungalled ones in three of four species*site combinations (Fig. 1b), but the difference was significant in paired *t* tests only for *S. gigantea* at Fredericton (*S. altissima*: Toronto $t_{(80)} = 0.13$, $P = 0.90$; Fredericton $t_{(60)} = -0.99$, $P = 0.33$; *S. gigantea*: Toronto $t_{(79)} = -1.83$, $P = 0.070$; Fredericton $t_{(74)} = -2.95$, $P = 0.004$). The galled-ungalled flower difference (GUFD) was larger for *S. gigantea* than for *S. altissima* at each site, paralleling the result for GUMD, although with the larger error variance the GUFD difference was not significant in 2-way ANOVA (Table 1b).

Biomass allocations to stem, leaf, and flower tissue showed a consistent pattern: allocation to stem tissue was larger, and allocations to leaf and flower tissue smaller, in galled ramets (Fig. 2). However, there was little detectable variation between species or between sites in the galled-ungalled allocation differences. A marginally significant species*site interaction for the galled-ungalled leaf allocation difference (Table 2a) appears driven by a GULAD that is smaller for *S. altissima* at Fredericton than otherwise, although the sign is the same for all species*site combinations. The galled-ungalled flower allocation difference showed no detectable variation between species or sites (Table 2b).

Discussion

While the difficulty of experimentally manipulating *G. gallaesolidaginis* attack prevents direct estimates of gallmaker impact on growth of the two host plants, our data indicate that these impacts can be large, and are much larger on the novel host (*S. gigantea*) than they are on the ancestral host (*S. altissima*). While we did not measure belowground impacts of herbivory, growth of new rhizomes is supported by export of photosynthate from aboveground tissues (Schmid et al. 1988b) and galled ramets of *S. altissima* maintain relative, not absolute, allocation of biomass to rhizome growth (Hartnett and Abrahamson 1979). Thus, we strongly suspect that a large impact on aboveground biomass translates into a large impact on asexual reproduction via rhizomes.
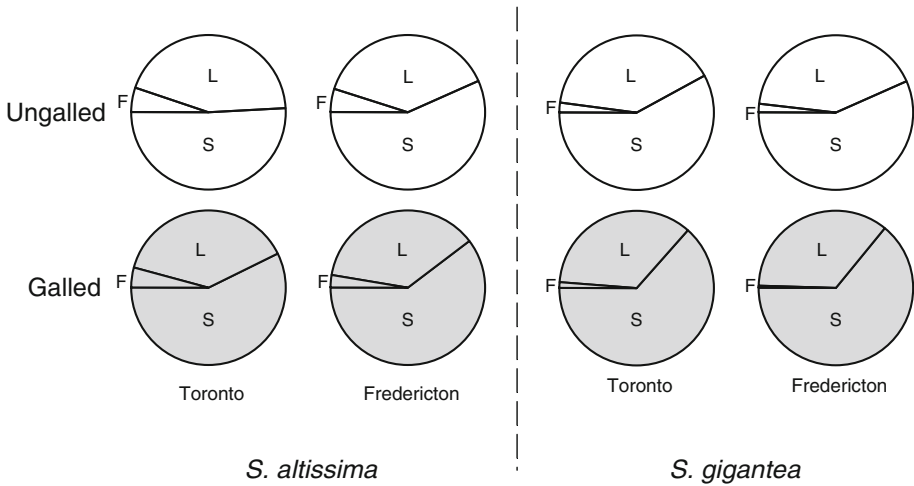
Fig. 2 Relative allocation of aboveground biomass investment to stems (S), leaves (L), and flowers (F) by galled and ungalled *S. altissima* and *S. gigantea*, at study sites in Toronto and Fredericton

	df	MS[a]	F	P
(a) GULAD (impact on allocation to leaves)				
Host species	1	17.8	1.35	0.25
Site	1	8.97	0.68	0.41
Species*site	1	55.7	4.21	**0.041**
Residual	293	13.2		
(b) GUFAD (impact on allocation to flowers)				
Host species	1	1.47	0.42	0.52
Site	1	5.54	1.59	0.21
Species*site	1	1.04	0.30	0.58
Residual	293	3.48		

Table 2 Analysis of (a) galled-ungalled leaf allocation difference (GULAD) and (b) galled-ungalled flower allocation difference (GUFAD) for *S. altissima* and *S. gigantea* at Toronto and Fredericton

[a] Entry is MS $\times 10^3$

The greater impact of *G. gallaesolidaginis* on *S. altissima* is consistent with predictions based on the expected evolution of higher tolerance (by the host plant) and of lower virulence (by the attacking insect) in the older association. The *Gnorimoschema-Solidago* system is one in which these expectations are particularly clear: there is little evidence for costs of tolerance in *S. altissima* (Hakes and Cronin 2011), and as a host-specialist, solitary, internally feeding herbivore *Gnorimoschema* fits none of the scenarios associated with the evolution of high rather than low virulence (e.g. Ewald 1994; Levin and Bull 1994; Nowak and May 1994; Mosquera and Adler 1998; Messenger et al. 1999; Vigneux et al. 2008; Alizon et al. 2009). What is less clear is whether the difference in impact we demonstrate between hosts results primarily from a difference in plant tolerance or in insect virulence, or indeed whether it is possible to separate the two (here, or ever; see Restif and Koella 2004 and Rohr et al. 2010 for divergent opinions). Gallmaker attack also reduced potential sexual reproduction (flower mass). As for ramet mass, the galled-ungalled difference in flower mass was larger for the novel host (*S. gigantea*), but the error variance for flower mass was much larger and so this difference between species was not statistically significant.

Perhaps surprisingly, *Solidago* tissue allocations were not greatly affected by gallmaker attack. The clearest pattern is that allocation to stem tissue is larger in galled ramets, at the expense of allocation to leaves and flowers. Much of this pattern likely arises simply because gallmakers preferentially attack thicker-stemmed ramets (Heard and Cox 2009), but we cannot exclude the possibility that the physical and chemical signals that drive gall morphogenesis influence stem development at some distance from the gall. We measured allocation because we hypothesized that *Solidago* under attack might allocate a larger fraction of resources to flowers, thus achieving more tolerance in sexual reproduction than in overall growth. Our data show no hint of this pattern for either the ancestral or novel association. However, reallocation toward flowers at the expense of leaves and stem would reduce the availability of photosynthates to new rhizomes, potentially compromising asexual reproduction via rhizomes. Because we did not collect underground tissues, we cannot further evaluate this potential tradeoff.

The association of *G. gallaesolidaginis* with *S. gigantea* is novel by comparison with its association with *S. altissima*, but is still of considerable age. Estimates based on divergence at mitochondrial COI suggest that genetic differentiation of *G. gallaesolidaginis* on *S. altissima* and *S. gigantea* began at least 300,000 years ago (and perhaps as long as 1.9 million years ago; Stireman et al. 2005), and presumably the host shift that began the interaction between *G. gallaesolidaginis* and *S. gigantea* is no younger than this. This represents at least 300,000 generations for the univoltine *G. gallaesolidaginis*, and a smaller but unknown number of generations for the long-lived perennial *S. gigantea*. This suggests a surprisingly long persistence of higher impact for the novel host association, especially given evidence for considerable response to selection by members of some exotic-native herbivore-host pairs on time scales of a few decades (e.g. Carroll et al. 1997, 2005; Abhilasha and Joshi 2009; Huang et al. 2010).

Evolutionary persistence of strong impact on the novel host could be accounted for if selection for increased tolerance and reduced virulence is weak in this system, or if constraints have prevented either host or herbivore from responding to selection. Both explanations are plausible, although we can only speculate about their importance in this system. We have not measured the strength of selection on tolerance in the *Solidago-Gnorimoschema* system, although it is possible that selection is relatively weak despite strong impacts of gallmakers on attacked ramets. *S. gigantea* and *S. altissima* are rhizomatous perennials that spread clonally, with genets often spatially extensive and including very large numbers of ramets (Maddox et al. 1989; S. Heard, pers. obs.). As a result, even the complete devastation of a ramet under attack may be only a mild insult to a genetic individual. Furthermore, in most populations attack rates on both hosts by *G. gallaesolidaginis* are low (very often <1%; S.B. Heard, unpubl. data), and Lau (2008, working with *Lotus wrangelianus*) showed that selection on tolerance weakens when insect attack is sparse. It is even possible that low attack rates on *S. gigantea* reflect the evolution of increased resistance after *G. gallaesolidaginis*'s host shift—and if resistance and tolerance trade off (Fornoni et al. 2004; Núñez-Farfán et al. 2007; Agrawal 2011; but see Jokela et al. 2000) then a response to selection in resistance might pre-empt a response in tolerance. We have not measured resistance to *G. gallaesolidaginis* by *S. altissima/gigantea*, although Hakes and Cronin (2011) found selection against resistance to leaf-chewing herbivores in *S. altissima* (and no evidence for resistance-tolerance tradeoffs). Finally, the strength of selection on *G. gallaesolidaginis* virulence will depend on how much its impact on *Solidago* is mediated by its sequestration of plant resources into gall and insect tissues, versus by incidental damage to young leaves, meristems, and vascular tissue during gall formation. Selection should be weak to reduce virulence via the former mechanism, but strong on

the latter, and while *G. gallaesolidaginis* inflicts both kinds of damage our data do not allow us to separate them.

It is also possible that constraints related to availability of heritable genetic variation or to attack phenology limit the evolution of plant tolerance and insect virulence in our system. Hakes and Cronin (2011) detected significant selection on *S. altissima* for increased tolerance to leaf-chewing herbivores, but measured very low heritability for tolerance and suggested this as a constraint on the evolution of tolerance. It is, however, unknown how tolerance of leaf-chewing relates to tolerance of gallmaking. Constraints on the evolution of virulence may also arise in the system, because the *Gnorimoschema* host forms on *S. altissima* and *S. gigantea* have diverged in numerous ecological traits, including timing of initial host attack (Seehawer 2002). Attack is significantly earlier on *S. gigantea*, and because plants are thus smaller when attacked, attack may be more likely to damage meristems and the loss of the same absolute amount of tissue may have a larger impact on subsequent growth. If the phenological offset plays a role in assurance of correct host targeting, then one avenue towards reduced virulence (later attack) may not be available for *G. gallaesolidaginis* on *S. gigantea*.

Of course, it will not be possible to fully understand the pace of adaptive evolution in novel herbivore-host systems from a single species triad (such as *G. gallaesolidaginis*— *S. altissima*—*S. gigantea*). While our study is well replicated at the individual-plant level, and we were able to replicate at the site level as well, we have examined only a single instance of host shifting. Two avenues for future research suggest themselves. First, we need data comparing impact on ancestral and novel hosts for herbivores on more host-plant pairs (because in any single case, novelty will be confounded with other differences between host species). Second, we can learn much from replication at the level of herbivore species on a given host pair. The *Solidago* system offers an outstanding opportunity to obtain such comparative data, because among the many insect herbivores attacking *S. altissima* and *S. gigantea* are at least two others with datable diet expansions adding *S. gigantea* as a novel host: *Eurosta solidaginis* (Diptera: Tephritidae) and *Rhopalomyia solidaginis/capitata* (Diptera: Cecidomyiidae). *E. solidaginis* has a host-race pair that is not likely more than 200,000 years old, and likely much younger, while the *Rhopalomyia* sister species are at least 2 million years old (Stireman et al. 2005). The impacts of *Eurosta* and *Rhopalomyia* on *S. altissima* have been well studied (Hartnett and Abrahamson 1979), but comparable data for *S. gigantea* are not available. Comparing herbivores that share a host-plant pair but differ in age of the novel association should offer a powerful approach to understanding the evolutionary history of new herbivore-host associations.

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