The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2010, **101**, 544–552. With 1 figure

Differential herbivory on disk and ray flowers of gynomonoecious asters and goldenrods (Asteraceae)

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Received 5 February 2010; revised 20 May 2010; accepted for publication 21 May 2010

The selective advantage of gynomonoecy, the sexual system wherein plants produce a mixture of female and bisexual flowers, is poorly understood. One hypothesis for the evolution of this system is that the absence of androecia from female flowers reduces herbivore damage to the gynoecia of these flowers. Here, we examined patterns of herbivore damage in 53 collections representing 25 species of asters and goldenrods from Massachusetts, USA. In these taxa flowers are crowded into compact capitula, with bisexual flowers occupying the centre and female flowers situated on the periphery. Damage to gynoecia of bisexual flowers was significantly greater than damage to gynoecia of female flowers overall, and in about half of the individual populations. We also compared damage to central and peripheral flowers in the heads of 16 collections of other Asteraceae that produce only bisexual flowers to see whether the location of flowers rather than their sex might determine the patterns of herbivory. In only one of these 16 collections did we find a significant difference in herbivory between flower positions. We conclude that herbivore damage is influenced by flower type in asters and goldenrods, a pattern consistent with a role for herbivory in the evolution and maintenance of gynomonoecy. © 2010 The Linnean Society of London, Biological Journal of the Linnean Society, 2010, **101**, 544–552.

ADDITIONAL KEYWORDS: capitulum – florivory – gynomonoecy – sexual system – *Solidago* – *Symphyotrichum*.

INTRODUCTION

Herbivory is a major selection pressure in flowering plants, acting on many plant attributes, including reproductive biology. Several studies suggest that herbivory on flowers (florivory) can be an important selective force in the evolution of sexual systems, including the evolution of dioecy from cosexuality (Bawa & Opler, 1978; Cox, 1982; Muenchow & Delesalle, 1992; Ashman, 2002), and the maintenance of females in gynodioecious species (Marshall & Ganders, 2001) and males in andromonoecious species (Muenchow, 1998). The impact of herbivory on sexual systems arises when the extent of damage differs between flowers, inflorescences, or plants that differ in sex expression. Such morph-specific herbivory has been documented in numerous dioecious or gynodioecious species, with male plants usually receiving more damage than female plants (summarized in Boecklen & Hoffman, 1993; Ågren *et al*., 1999; but see Strauss, 1990). Differential herbivory of male and female individuals may be directed towards flowers (Bawa & Opler, 1978; Cox, 1982; Boecklen, Price & Mopper, 1990; Krischik & Denno, 1990; Muenchow & Delesalle, 1992; Wolfe, 1997), or it may involve other plant parts, such as foliage, stems, or seeds (Danell *et al*., 1985; Ågren, 1987; Elmqvist & Gardfjell, 1988; Boecklen *et al*., 1990; Krischik & Denno, 1990; Boecklen & Hoffman, 1993; Wolfe, 1997; Marshall & Ganders, 2001).

Differential herbivory of flowers or inflorescences that differ in sex expression within a single plant has been reported less often. Herbivory on male flowers exceeded that on female flowers in monoecious *Psiguria warscewiczii* and *Sagittaria latifolia* (Murawski, 1987; Muenchow & Delesalle, 1992). However, damage to female flowers exceeded damage to male flowers in *Pinus edulis* (Cobb, Trotter & Whitham, 2002). Damage to female flowers in *Freycinetia*

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*Corresponding author. E-mail: rbertin@holycross.edu *reineckei* was greater if they occurred in bisexual inflorescences than if they occurred in female inflorescences (Cox, 1982).

Whereas patterns of herbivory in relation to sexual system have been examined in dioecious, monoecious, and gynodioecious species, the relevance of herbivory to gynomonoecy remains unexplored. Gynomonoecy is a sexual system in which individual plants produce both female and bisexual flowers. This system is widespread in the Asteroideae, the largest subfamily in the Asteraceae, and several surveys report its occurrence in 2.8–7.0% of angiosperms (Yampolsky & Yampolsky, 1922; Carlquist, 1974; Bernadello *et al.*, 2001; Lu & Huang, 2006).

Several possible adaptive advantages have been suggested for gynomonoecy (Willson, 1983; Bertin & Kerwin, 1998; Bertin & Gwisc, 2002). One hypothesis states that gynomonoecy is beneficial because it removes some gynoecia from the vicinity of androecia, and thereby reduces herbivore damage to pistils. Such a pattern might occur, for example, if herbivores were attracted to pollen but additionally caused damage to pistils if these were present in the same flower. Under these conditions, plants producing some of their gynoecia in female flowers (gynomonoecious individuals) would have higher maternal fitness than plants that produced all of their gynoecia in bisexual flowers. A prediction of this hypothesis is that gynoecial damage is greater in bisexual flowers than in female flowers. In this study we evaluate this expectation by comparing the frequencies of gynoecial damage in ray and disk flowers in 25 species of gynomonoecious asters and goldenrods.

MATERIAL AND METHODS

STUDY SPECIES AND FIELD COLLECTIONS

The terms aster and goldenrod refer here to taxa that at one time were assigned to the genera *Aster* and *Solidago*, respectively. Taxonomic studies have since split each taxon into multiple genera. Asters used in this study are currently assigned to the genera *Doellingeria*, *Eurybia*, *Ionactis* and *Symphyotrichum*. Goldenrods now belong to the genera *Euthamia* and *Solidago*. All asters and goldenrods are in tribe Astereae of the subfamily Asteroideae. Asters and goldenrods produce numerous small flowers aggregated into heads, or capitula. Within a capitulum, an outer ring of female flowers surrounds an inner group of bisexual disk flowers. In most taxa, each female (ray) flower bears a single conspicuous petal, or ray. The entire capitulum resembles a single large flower (Leppik, 1977).

We made 13 collections of gynomonoecious species within 25 km of Worcester, Massachusetts (centred around 42.27°N, 71.81°W) during the late summer and autumn of 2002, six in 2003, and 34 in 2007. Sixteen collections of composites with exclusively bisexual flowers were made during the same period. The typical procedure was to walk through a population, collecting from the closest plant every 1–2 m (depending on the species) along the way. We collected from up to 20 plants if sufficient individuals were available. Multiple heads were collected from scattered locations on each plant and preserved in alcohol. To control for developmental stage, heads were selected only if they were old enough that every flower in the head had opened, but not so old that perianths had detached or pappi were conspicuous.

In addition to the 53 collections of asters and goldenrods, we collected heads from 16 populations representing ten species of composites that produce exclusively bisexual flowers. These collections were made to evaluate the effect of position of flower within the head. Position is a potentially confounding variable in this study because ray flowers are always peripheral and disk flowers are always central in asters and goldenrods. Collected species containing only bisexual flowers included members of the genera *Eupatorium* and *Eutrochium* in the tribe *Eupatoriae* of the subfamily *Asteroideae*, and *Hieracium*, *Lactuca*, *Scorzoneroides*, *Taraxacum*, and *Tragopogon* in the tribe Cichorieae of the subfamily Cichorioideae (Table 1).

We examined between one and five heads per plant under a dissecting microscope. The number was constant for plants in a given population, and was influenced by the number of heads of a suitable developmental stage at the time of collection. For gynomonoecious species, we recorded the numbers of ray and disk flowers with ovary damage, and the numbers with either stigma or style damage. A stigma was scored as damaged if at least half of it was missing. Styles scored as damaged were typically severed. For species with bisexual flowers we removed the outermost ring of flowers from each head and treated these as 'outer' flowers, in contrast to the remaining 'inner' flowers. Ovary damage in each group was recorded separately. We did not record stigma damage for members of the tribe Cichorieae because most of the stigmas had separated from the ovaries by the time of counting, rendering it impossible to distinguish the stigmas of inner and outer flowers. Stigma/style damage was tallied for the remaining two species with bisexual flowers (genera *Eupatorium* and *Eutrochium*). In total, we examined 3654 heads and over 117 000 flowers from gynomonoecious species, and 805 heads and over 22 000 flowers from species with bisexual flowers only.

Table 1. Collection information for composites examined in this study. Numbers after species names denote different populations. The collection no. is used for reference in Figure 1. Plants and heads refer to the numbers of sampled plants and numbers of heads per plant, respectively

Gynomonoecious asters and goldenrods	Collection no.	Year	Plants	Heads
Doellingeria umbellata (P. Mill.) Nees 1	1	2002	20	2
Doellingeria umbellata (P. Mill.) Nees 2	2	2002	15	2
Doellingeria umbellata (P. Mill.) Nees 3	3	2007	20	3
Doellingeria umbellata (P. Mill.) Nees 4	4	2007	20	3
Eurybia divaricata (L.) Nesom 1	5	2002	20	2
Eurybia divaricata (L.) Nesom 2	6	2007	20	3
Eurybia divaricata (L.) Nesom 3	7	2007	20	3
Euthamia graminifolia (L.) Nutt. 1	8	2007	20	5
Euthamia graminifolia (L.) Nutt. 2	9	2007	19	5
Ionactis linariifolius (L.) Greene 1	10	2002	20	1
Ionactis linariifolius (L.) Greene 2	11	2007	20	3
Solidago altissima L. 1	12	2002	20	3
Solidago altissima L. 2	13	2007	18	5
Solidago altissima L. 3	14	2007	20	5
Solidago arguta Ait.	15	2003	19	4
Solidago bicolor L. 1	16	2002	20	3
Solidago bicolor L. 2	17	2003	15	4
Solidago bicolor L. 3	18	2007	20	5
Solidago caesia L.	19	2007	20	5
Solidago gigantea Ait.	20	2007	20	5
Solidago juncea Ait. 1	21	2003	20	5
Solidago juncea Ait. 2	22	2007	20	5
Solidago nemoralis Ait. 1	23	2007	20	5
Solidago nemoralis Ait. 2	24	2007	20	5
Solidago odora Ait.	25	2007	20	5
Solidago puberula Nutt. 1	26	2002	20	3
Solidago puberula Nutt. 2	27	2007	9	5
Solidago rugosa P. Mill. 1	28	2003	20	5
Solidago rugosa P. Mill. 2	29	2007	18	5
Solidago rugosa P. Mill. 3	30	2007	20	5
Solidago rugosa P. Mill. 4	31	2007	20	5
Solidago sempervirens L.	32	2007	20	5
Solidago uliginosa Nutt.	33	2007	18	5
Symphyotrichum cordifolium (L.) Nesom	34	2007	20	3
Symphyotrichum ericoides (L.) Nesom 1	35	2002	20	2
Symphyotrichum ericoides (L.) Nesom 2	36	2007	20	3
Symphyotrichum laeve (L.) A. & D. Löve 1	37	2002	20	2
Symphyotrichum laeve (L.) A. & D. Löve 2	38	2007	18	3
Symphyotrichum lanceolatum (Willd.) Nesom	39	2007	20	3
Symphyotrichum lateriflorum (L.) A. & D. Löve 1	40	2003	18	3
Symphyotrichum lateriflorum (L.) A. & D. Löve 2	41	2007	20	3
Symphyotrichum novae-angliae (L.) Nesom 1	42	2002	20	2
Symphyotrichum novae-angliae (L.) Nesom 2	43	2002	20	2
Symphyotrichum novae-angliae (L.) Nesom 3	44	2007	20	3
Symphyotrichum novae-angliae (L.) Nesom 4	45	2007	19	3
Symphyotrichum pilosum (Willd.) Nesom	46	2007	20	3
Symphyotrichum puniceum (L.) A. & D. Löve 1	47	2002	20	2
Symphyotrichum puniceum (L.) A. & D. Löve 2	48	2003	20	3
Symphyotrichum puniceum (L.) A. & D. Löve 3	49	2007	20	3
Symphyotrichum puniceum (L.) A. & D. Löve 4	50	2007	20	3
Symphyotrichum racemosum (Ell.) Nesom 1	51	2002	20	2
Symphyotrichum racemosum (Ell.) Nesom 2	52	2007	19	3

Table 1. *Continued*

Gynomonoecious asters and goldenrods	Collection no.	Year	Plants	Heads
Symphyotrichum racemosum (Ell.) Nesom 3	53	2007	17	3
Composites with bisexual flowers				
Cichorium intybus L.		2003	15	3
Eutrochium dubium (Willd. ex. Poir.) E.E. Lamont		2007	19	3
Eupatorium perfoliatum L.		2007	20	3
Hieracium paniculatum L. 1		2003	20	4
Hieracium paniculatum L. 2		2003	19	4
Hieracium scabrum Michx. 1		2003	16	4
Hieracium scabrum Michx. 2		2003	20	2
Lactuca biennis (Moench) Fern. 1		2003	7	5
Lactuca biennis (Moench) Fern. 2		2003	19	4
Lactuca canadensis L. 1		2003	20	4
Lactuca canadensis L. 2		2003	20	4
Scorzoneroides autumnalis (L.) Moench 1		2003	20	1
Scorzoneroides autumnalis (L.) Moench 2		2003	20	1
Scorzoneroides autumnalis (L.) Moench 3		2007	20	2
Taraxacum officinale G.H. Weber		2003	20	1
Tragopogon dubius Scop.		2003	7	3

DATA ANALYSIS

We first calculated the percentage of ray and disk flowers (and inner and outer flowers) with stigma/style damage and (separately) with ovary damage in each head. We then calculated plant means for the proportion of flowers damaged in each category (ray, disk, inner, and outer). These data were not amenable to parametric analysis because many plants in some populations showed no damage, and the data could not be transformed to produce normally distributed residuals. We therefore used a non-parametric test on paired data for each population (Wilcoxon signed ranks test) to compare damage to disk and ray flowers. We performed 106 initial analyses, one each for stigma/style damage and ovary damage for each of the 53 collections. Although these analyses have the advantage of being performed at the level (population) relevant to the selective forces being investigated, they have two potential problems: the expectation of five or six significant results in 106 tests by chance (at $P = 0.05$), if all tests are independent, and the possibility that tests are not independent. The latter possibility reflects the fact that some collections were made in the same year, some were of the same species, and some genera were represented by multiple species.

We addressed the first issue by comparing the number of significant results with the expectation of five or six. We performed two additional analyses in attempting to address the second issue. In these analyses we used the difference in damage between disk and ray flowers in each population as the variable of interest. This quantity has the benefit of retaining comparison at the level of the population in all subsequent tests involving aggregated data. In the first analysis, we calculated species means separately for the three years of collection. Following Kolmogorov–Smirnov tests to assess normality, we compared the group of species means from each year with a hypothesized value of zero using a one-sample Student's *t*-test. Although it would also be desirable to control for species relatedness by presenting an analysis based on phylogenetically independent contrasts, such an analysis is not possible because the relationships among taxa in the different genera of asters and goldenrods are poorly understood, reflecting the low degree of variation among species and the uncertain placement of the many polyploid species (Brouillet *et al.*, 2006; J.C. Semple, pers. comm.). We partially addressed the lack of phylogenetic independence by conducting additional one-sample Student's *t*-tests using genus means, each calculated over all species in that genus. One such test was carried out on ovary damage and another on stigma/style damage.

We compared damage to ovaries of inner and outer flowers in those species with all bisexual flowers using a single Wilcoxon's test for each population, and similarly compared stigma/style damage in those two species for which we have data. We additionally performed a single overall analysis of ovary data in which we treated each collection as a single data point, without separating by year or calculating species averages. This approach is conservative for our 'control' data because its assumption of independence yields the greatest likelihood of detecting any difference (which, if found, would cause us to attribute any differences in gynomonoecious species to position rather than, as we hypothesize, to floral sex).

RESULTS

Levels of gynoecial damage ranged from none in several samples to a high of 20–30% of flowers in others (Fig. 1; Table 2). In some flowers damage was focused on the stigma, with part or all removed, sometimes along with adjacent parts of the style. Occasionally the style was severed without damage to the stigma. Such damage could have resulted either from insect larvae or from a mobile adult herbivore, such as a beetle, on the surface of the capitulum. Ovary damage was caused principally by small insect larvae (especially Lepidoptera, but including some Diptera and Coleoptera). Some small larvae bored into the ovary, consuming it from the inside. Larger larvae attacked from the outside, typically eating through multiple ovaries and often damaging other flower parts as well.

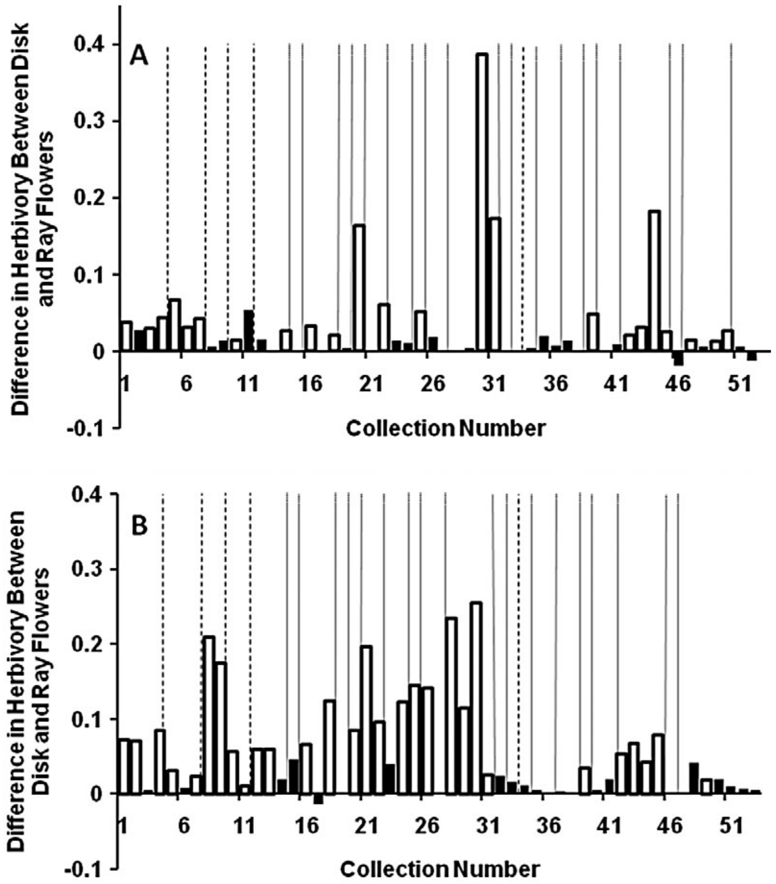

Figure 1. A, differences in herbivory to ovaries of disk and ray flowers, calculated as proportion of disk ovaries damaged minus proportion of ray ovaries damaged. Positive values thus denote herbivory to disk flowers that exceeds herbivory to ray flowers. B, differences in herbivory to stigmas and styles of disk and ray flowers, calculated as above. Significant differences between disk and ray damage are denoted by white columns. Dotted vertical lines separate data for different species; heavier dashed lines separate data for different genera. Collection numbers (see Table 1) represent the following species and populations. 1–4, *Doellingeria umbellata* 1, 2, 3, and 4; 5–7, *Eurybia divaricata* 1, 2, and 3; 8 and 9, *Euthamia graminifolia* 1 and 2; 10 and 11, *Ionactis linariifolius* 1 and 2; 12–14, *Solidago altissima* 1, 2, and 3; 15, *Solidago arguta*; 16–18, *Solidago bicolor* 1, 2, and 3; 19, *Solidago caesia*; 20, *Solidago gigantea*; 21 and 22, *Solidago juncea* 1 and 2; 23 and 24, *Solidago nemoralis* 1 and 2; 25, *Solidago odora*; 26 and 27, *Solidago puberula* 1 and 2; 28–31, *Solidago rugosa* 1, 2, 3, and 4; 32, *Solidago sempervirens*; 33, *Solidago uliginosa*; 34, *Symphyotrichum cordifolium*; 35 and 36, *Symphyotrichum ericoides* 1 and 2; 37 and 38, *Symphyotrichum laeve* 1 and 2; 39, *Symphyotrichum lanceolatum*; 40 and 41, *Symphyotrichum lateriflorum* 1 and 2; 42–45, *Symphyotrichum novae-angliae* 1, 2, 3, and 4; 46, *Symphyotrichum pilosum*; 47–50, *Symphyotrichum puniceum* 1, 2, 3, and 4; 51–53, *Symphyotrichum racemosum* 1, 2, and 3.

Table 2. Gynoecial damage to outer and inner flowers of capitula in composites with bisexual flowers. All numbers represent the proportion of ovaries damaged, except for the second number listed for *Eupatorium* and *Eutrochium*, which designates the proportion of stigmas and styles damaged

	Gynoecium damage	
	Outer	Inner
Cichorium intybus	0.000	0.000
Eutrochium dubium	0.000/0.248	0.000/0.301
Eupatorium perfoliatum	0.002/0.241	0.004/0.236
Hieracium paniculatum 1	0.000	0.000
Hieracium paniculatum 2	0.000	0.000
Hieracium scabrum 1	0.073	0.080
Hieracium scabrum 2	0.000	0.001
Lactuca biennis 1	0.061	0.073
Lactuca biennis 2	0.000	0.000
Lactuca canadensis 1	0.123*	0.147
Lactuca canadensis 2	0.124	0.089
Scorzoneroides autumnalis 1	0.012	0.041
Scorzoneroides autumnalis 2	0.003	0.003
Scorzoneroides autumnalis 3	0.009	0.004
Taraxacum officinale	0.013	0.008
Tragopogon dubius	0.000	0.000

*Differences significant at $P < 0.05$.

Pistils of disk flowers experienced higher levels of damage than pistils of ray flowers, illustrated by the striking excess of positive over negative values in Figure 1. Under the assumption of independence, the likelihood of obtaining results this skewed by chance is vanishingly small ($< 10^{-9}$ for ovary damage and $< 10^{-13}$ for stigma/style damage). Stigma/style damage was significantly greater in disk than ray flowers in 29 of 53 populations, and ovary damage was significantly greater in disk than ray flowers in 23 of these populations (Fig. 1). In no population did damage to ray flowers significantly exceed damage to disk flowers. Of the three analyses of data from individual years (Table 3), damage to both ovaries and stigmas in 2002 and 2007 was significantly higher in disk flowers than in ray flowers ($P < 0.01$ in each analysis, significant after applying a Bonferroni correction for multiple tests). Levels of damage to ray and disk flowers were not significantly different in 2003, although the sample size in this year was lower ($n = 6$) than in other years, and therefore the test was not very powerful. The trend for both ovary and stigma damage was, however, consistent with those in other years. The final analysis, performed at the level of the genus, revealed significantly higher ovary damage among disk flowers than among ray flowers ($P = 0.004$, significant after Bonferroni correction), but no significant difference between flower types in damage to stigmas and styles ($P = 0.057$). The small sample size ($n = 6$) means that these tests have low power and are capable of demonstrating only very large differences.

Table 3. Damage to ray and disk flowers in each of three years. The dependent variable is the difference in proportion of disk and ray flowers damaged, with a positive value indicating greater damage to disk flowers. The mean difference is calculated over all species sampled in that year

	Mean difference in damage Disk–Ray	N	t	P
2002				
Ovary damage	0.023	11	4.73	0.001
Stigma damage	0.046	11	3.619	0.005
2003				
Ovary damage	0.001	6	1.000	0.363
Stigma damage	0.085	6	1.999	0.102
2007				
Ovary damage	0.034	24	3.245	0.004
Stigma damage	0.048	24	4.379	< 0.001

Only one of the 16 collections with exclusively bisexual flowers showed a significant difference in ovary damage between inner and outer flowers (Table 2), typical of what would be expected by chance. Among the 15 populations not showing a significant difference between inner and outer flowers, no consistent pattern was evident in the data, with inner flowers suffering more damage than outer flowers in six collections, less in three, and the same in seven. Neither of the two species that retained stigmas (*Eutrochium dubium* and *Eupatorium perfoliatum*) showed a significant difference in stigma/style damage between inner and outer flowers (Table 2), with a higher sample mean for inner flowers in one species and for outer flowers in the other.

DISCUSSION

The results show a pervasive pattern of greater damage to the gynoecia of bisexual disk flowers than to the gynoecia of female ray flowers in a large sample of local asters and goldenrods. This pattern is evident in the overall analysis, as well as in significant test results involving nearly half of the individual populations. An analysis of species means in three different years revealed significant disk/ray differences in two years. Finally, overall tests on genus means reveal significantly greater damage to ovaries of disk than ray flowers, and a difference in stigma/style damage that approaches significance. It should be noted that all the above tests employed a two-tailed alternate hypothesis. Had a one-tailed alternate hypothesis been employed, which could be justified by the clearly directional nature of the biological hypothesis, an even greater number of the tests would have been significant.

Two concerns discussed above regarding data analysis are: (1) the likelihood of several significant tests occurring by chance among the 106 tests performed on individual populations; and (2) the lack of independence in several aspects of the data. The first issue was addressed by the far greater number of significant tests (52) than the five or six expected by chance. The second issue was addressed by performing additional tests intended to minimize the effects caused by non-independence related to year, multiple samples from certain species, and non-independence of species. These tests reveal patterns similar to those at the population level. Also worth noting is that considerable differences exist among herbivory levels within some species, and within the two genera that contain multiple species (*Solidago* and *Symphyotrichum*) (Fig. 1), suggesting that a considerable degree of independence in damage may exist among collections.

The greater damage to gynoecia of disk flowers than of ray flowers could be related either to floral sex or to the different locations of ray and disk flowers within capitula. However, the absence of a difference between outer and inner flowers in taxa with only bisexual flowers suggests that sexual differences rather than positional differences of the two flower types in the capitulum were the more likely cause. A caveat here is that our 'controls' were not perfect in that the species involved were necessarily different, and most belonged to a different subfamily of the Asteraceae.

A possible explanation of the differences in herbivory to ray and disk flowers is that herbivores are attracted to pollen, and that damage to gynoecia is either incidental or at least secondary to the initial attraction to pollen. This seems likely for damage to stigma and style because of the mechanism of pollen presentation in these species. Disk flowers discharge pollen into the tube formed by the disk corolla. Elongation of the style causes the stigma to push this pollen out of the end of the corolla tube in the manner of a piston, coating the outer surfaces of the stigma in the process. Because pollen has a high nutritional value (Faegri & van der Pijl, 1979), this coating could potentially attract herbivores (e.g. Gross & Werner, 1983), and lead to damage of the stigma or the style. The greater damage to ovaries of disk compared with ray flowers seems less likely to result from incidental damage caused by pollen feeders, and what causes insects to attack disk ovaries preferentially is unclear.

Whatever the cause, the results exhibit a pattern that is consistent with a role for insect herbivory in the evolution and maintenance of gynomonoecy in these plants. When herbivores preferentially attack the gynoecia of bisexual flowers compared with the gynoecia of female flowers, plants that produce some female flowers will have higher maternal fitness than plants producing only bisexual flowers. The net value of this pattern to a plant will be the difference between the maternal fitness gain resulting from increased seed production and the loss of paternal fitness resulting from the lack of pollen production in female flowers. As bisexual flowers become less common in a population they are likely to become more valuable to the plants that bear them because collectively they necessarily provide the entire paternal contribution to the seeds of the population. Such value would presumably lead either to the retention of some bisexual flowers on each plant, as in asters and goldenrods, or to the specialization of individuals as males and females (i.e. the evolution of dioecy; Willson, 1979).

Gynomonoecy seems to have arisen from at least two other sexual systems (hermaphroditism and monoecy), and in turn to have given rise to plants exhibiting hermaphroditism, monoecy, trioecy, and dioecy (Lloyd, 1972; Torices, 2009; Torices & Anderberg, 2009). Previous papers summarized five hypotheses to account for the evolution of gynomonoecy from hermaphroditism in the Asteraceae (Bertin & Kerwin, 1998; Bertin & Gwisc, 2002). Of these hypotheses, one is the herbivory hypothesis tested in this paper. A second is that gynomonoecy reduces inbreeding depression by favouring out-crossing, particularly where it occurs together with interfloral protogyny (Burtt, 1977; Willson, 1983; Abbott & Schmitt, 1985). This is unlikely for asters and goldenrods because these taxa exhibit physiological self-incompatibility (Mulligan & Findlay, 1970; Jones, 1978; Gross & Werner, 1983; Bertin & Kerwin, 1998). A third explanation is that gynomonoecy reduces pollen–pistil interference. To our knowledge, this has not been tested. A fourth explanation is that the two flower types permit flexibility in allocation of resources to male and female functions (Lloyd, 1979; Willson, 1983). Earlier work (Bertin & Kerwin, 1998; Bertin & Gwisc, 2002) suggests, however, that ratios of flower types do not change in response to environmental conditions in asters and goldenrods. The final explanation is that the presence of showy rays on female flowers increases pollinator attraction (Leppik, 1977; Bawa & Beach, 1981), thereby compensating for any loss in fitness resulting from reduced pollen production. The existence of an evolutionary trade-off between rays and stamens is supported by the phylogenetic analysis of Torices & Anderberg (2009). Thus, of the five hypotheses, two (inbreeding reduction and sex allocation) seem unlikely, one (herbivory) is supported by the data in this paper, and the other two await further evaluation.

In sum, data presented in this paper reveal striking differences in herbivore damage to pistils of female and bisexual flowers of asters and goldenrods. This pattern is consistent with a role for herbivory in the evolution and maintenance of gynomonoecy. Our understanding of the gynomonoecious sexual system would benefit from research examining other hypotheses concerning its origin, studies of gynomonoecious taxa outside the Asteraceae, and phylogenetic analyses providing further information on evolutionary transitions of sexual systems in families containing gynomonoecious species.

ACKNOWLEDGEMENTS

The authors thank the College of the Holy Cross for financial support, C. Gibson for help in analysing data, A. Ellison and E. Farnsworth for discussions of data analysis, W. Duan for translating the article by Lu and Huang, and several reviewers for helpful comments.

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