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Floral sex ratios and gynomonoecy in *Solidago* (Asteraceae)

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Received 22 April 2002; accepted for publication 29 August 2002

Gynomonoecy is the sexual system in which individual plants bear both female and bisexual flowers. Little attention has been paid to the adaptive significance of this sexual system, which is particularly prevalent in the Asteraceae. We investigated one hypothesized advantage of having two flower types, namely that this arrangement permits flexibility in allocation of resources to male and female reproductive functions. We examined six species of goldenrod (*Solidago*), a genus of gynomonoecious, perennial herbs. In greenhouse experiments, we varied one or more of three environmental variables – light, nutrients and water – and/or examined heads in different positions on the plants. Most variables had little or no effect on the proportion of ray flowers. Significant effects were found for light in 0 of 5 experiments, for nutrients in 4 of 9 experiments and for water in 0 of 3 experiments. Heads in different positions in the inflorescence differed in the proportion of ray flowers in half of the experiments, though the differences were small. We also monitored temporal patterns in four species and found that the proportion of ray flowers increased significantly over the blooming period and the number of flowers per head declined. Because of the small number of significant effects and their modest magnitude, we conclude that the presence of two flower types in goldenrods is probably not advantageous in allowing flexibility in sex expression. It seems likely that this sexual system has been more important either in increasing pollinator attraction or in reducing pollen–pistil interference. The small observed changes in floral ratios were generally accompanied by changes in disc size in a manner consistent with an explanation based on allometry. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 413–422.

ADDITIONAL KEYWORDS: Allometry – capitulum – disc flowers – goldenrods – pollen–pistil interference – ray flowers – sex allocation – sex expression – sexual system.

INTRODUCTION

Angiosperms exhibit a diversity of sexual systems. In recent decades, much progress has been made in understanding the adaptive value of dioecy, monoecy, andromonoecy and gynodioecy (Willson, 1983; Richards, 1986; references therein). Less attention has been paid to gynomonoecy, the sexual system in which plants bear both female and bisexual flowers. This sexual system occurs in c. 2.8% of flowering plants (Yampolsky & Yampolsky, 1922), and is especially common in the Asteraceae.

One possible adaptive explanation of gynomonoecy is that the presence of two flower types (dichiny) permits flexibility in allocation of resources to male and female reproductive functions in response to variation

in environmental factors. Such variation in sex expression could be advantageous because male and female sexual functions are subject to somewhat different selection pressures and can be most effective under different circumstances (Charnov & Bull, 1977; Willson, 1983).

A common expectation is that the female function should be emphasized under conditions of high resource availability and maleness when resources are scarcer or the environment is harsher. This difference reflects the presumption that female reproductive success is usually limited by the availability of resources for making fruits and seeds, while male success is more likely to be limited by access to ovules (Bateman, 1948; Janzen, 1977). In fact, many monoecious and andromonoecious species show a female emphasis in high light and high nutrient conditions (Gregg, 1975, 1978; Bertin, 1982; Solomon, 1985, 1989; Cid-Benevento, 1987; Emms, 1993). Similarly,

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greater male sex expression has been linked to dry conditions in several diclinous species (Barker, Freeman & Harper, 1982; Freeman, Klikoff & Harper, 1981; Schlessman, 1982; Stromberg & Patten, 1990), and males of some dioecious species are more likely to occupy xeric habitats than females (Freeman *et al.*, 1976; Dawson & Ehleringer, 1993). However, exceptions exist to all these patterns (Gregg, 1978; Lovett Doust & Harper, 1980; Lovett Doust, 1980 May & Spears, 1988).

Other patterns observed in some diclinous species are differences in sex expression over the course of the flowering season and on different parts of a plant. Seasonal changes include both increases and decreases in female sex expression (Lloyd, Webb & Primack, 1980; Primack & Lloyd, 1980; Coleman & Coleman, 1982; Willson & Ruppel, 1984; May & Spears 1988; Mossop, Macnair & Robertson, 1994; Méndez, 1998; references therein). Spatial variation in sex expression within an inflorescence or in different parts of a plant has been documented in numerous species (Freeman *et al.*, 1981; Bertin, 1982; Solomon, 1985; Diggle, 1991). Such differences have been attributed to different optimal locations for exporting pollen and for bearing fruit as a result of differential access to wind (in wind-pollinated species), light or photosynthate. Still other factors, such as plant size, herbivory, defoliation and past reproductive history, have also been linked to changes in sex expression (Ackerly & Jasienski, 1990; Bierzychudek, 1984; Méndez, 2001), although these variables are not considered here.

Our goals in this study were to determine whether changes in the ratios of the two flower types in gynodioecious goldenrods occur in response to variation in light, nutrient or water availability, and to determine whether sex expression varies with date or position on the plant. The presence of such changes would be consistent with the view that dicliny in these plants is advantageous in permitting flexibility in allocation of resources to male and female functions. We approached these questions by monitoring plants in the field and greenhouse for effects of date and by undertaking experimental manipulations of greenhouse-grown plants. We collected data not only on the proportion of ray flowers but also on the numbers of flowers per head with the expectation that this second variable might be affected by resource availability and would help interpret results involving sex expression.

MATERIAL AND METHODS

GOLDENRODS

Goldenrods (*Solidago* spp., Asteraceae) are herbaceous perennial plants, with most of the roughly 80 species found in North America (Mabberly, 1997). They bloom

in late summer or fall and are gynodioecious. Flowers are borne in small heads, or capitula, which in turn are arrayed in terminal panicles or thyrses – elongated inflorescences consisting of a main axis and numerous side branches, which are themselves usually branched (Fig. 1). In each head, several ray (female) flowers, each bearing a single petal, surround a small cluster of bisexual (disc) flowers. Within a head, the ray flowers open before the disc flowers. Each disc flower is protandrous, with pollen presentation preceding stigma receptivity (Müller, 1883; Gross & Werner, 1983).

FIELD AND GREENHOUSE METHODS

We observed the effects of date on flower number per head and on the proportion of ray flowers in four species: *S. nemoralis*, *S. puberula*, *S. rugosa* and *S. speciosa*. Observations of *S. nemoralis* and *S. rugosa* were made in 2000 in Paxton, Massachusetts, USA (42°18' N, 71°56' W) in an old field being invaded by woody species. Ten scattered individuals of each species were selected and marked before flowering. We visited the plants every 3–4 days through the flowering period and on each date we collected 10 flowering heads (or fewer if 10 were not available) from scat-

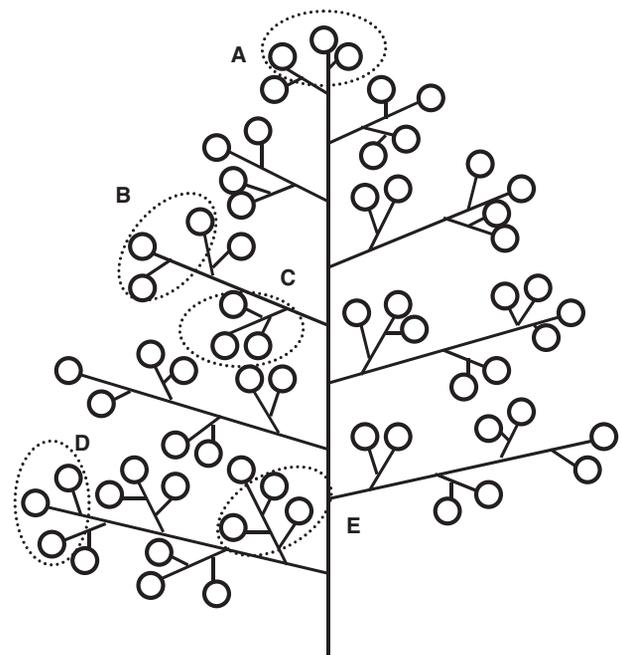


Figure 1. Simplified representation of a goldenrod inflorescence. Circles represent flowering heads, which usually number in the hundreds or thousands. A–E are the sampling positions in experiments in which five positions were sampled. For experiments in which only two positions were sampled, these were A and branch D–E.

Table 1. Summary of greenhouse experiments and field observations

Species and experiment number	Number of sibships†	Number of plants of each sibship in each treatment	Environmental variables‡	Heads harvested by position or date?	Number of heads harvested per plant§
<i>S. bicolor</i> , 1	12	6	L, N	P	10
<i>S. bicolor</i> , 2	12	2	L, N	P	10
<i>S. caesia</i>	9	3	L	P	25
<i>S. nemoralis</i> , 1	6	2	N	–	10
<i>S. nemoralis</i> , 2	12	1	N	P	20
<i>S. nemoralis</i> , 3	9	–	–	D	1–10
<i>S. odora</i> , 1	2	5	N, W	P	10
<i>S. odora</i> , 2	2	4	N, W	P	20
<i>S. puberula</i> , 1	9	1	–	P	25
<i>S. puberula</i> , 2	8	2	N, L	–	5
<i>S. puberula</i> , 3	12	1	–	P	20
<i>S. puberula</i> , 4	10	–	–	D	1–10
<i>S. rugosa</i>	9	–	–	D	1–10
<i>S. speciosa</i> , 1	9	1	N, W	P	20
<i>S. speciosa</i> , 2	2	2	N, L	P	20
<i>S. speciosa</i> , 3	12	–	–	D	1–10

†For observations of date, this column gives the number of plants monitored.

‡N = nutrients, L = light, W = water.

§Total number per plant except for experiments harvested by date, in which case the daily total is given.

tered locations on each plant. For consistency, we collected only heads with at least one but not all disc flowers open.

The effects of date on flowering in the remaining two species were examined in a greenhouse using plants grown from seeds collected in the field. We collected seeds of *S. puberula* from Worcester, Massachusetts (7 km east of Paxton) in 1996 and seeds of *S. speciosa* in 1998 from Brookfield, Massachusetts (20 km southwest of Paxton). Seeds were sown in vermiculite and kept moist over the winter in an unheated greenhouse. We transferred germinating seedlings to individual 20-cm pots containing Metromix 350, a soil-less growing medium. We watered and fertilized plants as needed to maintain vigorous growth. Ten plants of *S. puberula* and 12 plants of *S. speciosa* were selected before flowering and heads were collected from each plant as described above.

We conducted greenhouse experiments using varied levels of light, water and/or nutrients using six species: *S. bicolor*, *S. caesia*, *S. nemoralis*, *S. odora*, *S. puberula* and *S. speciosa*. We collected seeds of each species from natural populations within a 20 km radius of Paxton, Massachusetts. Seeds from each field-grown plant were kept separate and the seedlings arising from these different plants are referred to as sibships. We germinated seeds and raised seedlings as described above, and randomly assigned plants to experimental treatments in June. Plants

flowered either in the year of seedling emergence or in the next year, depending on the species.

We ran ten experiments, each using one of the above species. The experiments differed in whether light, nutrients, water or some combination were included as treatments, in the number of plants and sibships employed, and in the number of heads scored per plant (Table 1). These differences reflected in part the availability of plants and greenhouse space. Where light was manipulated, the two light levels were full ambient light and 50% full light, with the reduction obtained using shade cloth. Where nutrients were manipulated, the high nutrient treatment resulted from weekly fertilizations with a 50 p.p.m. solution of Peters 20–20–20 fertilizer, while low nutrient plants received an equal amount of fertilizer once per month. Where water was manipulated, plants in the high water treatment received sufficient water to keep the growth medium moist at all times, while plants in the low water treatment were allowed to dry to the point of wilting between treatments. If heads were harvested from one position, for consistency this position was at the tip of the central axis of the inflorescence. When heads were harvested from multiple positions, these were either two (tip of the central axis and from the lowest branch of inflorescence) or five (tip of plant, tip and base of lowest branch of inflorescence, and tip and base of middle branch in inflorescence; Fig. 1). During the period before flowering, the pots contain-

ing plants within a given experiment were rotated among positions in the greenhouse to minimize location effects. The numbers of ray and disc flowers on collected heads were counted under a dissecting microscope.

DATA ANALYSIS

We transformed all proportions by arcsine square root before further analysis. Reported means were back-transformed.

Experiments were designed with balanced sample sizes to be analysed with different models of ANOVA. Light, nutrients, water, date, and head position were treated as fixed effects. Plant and sibship were random factors, crossed or nested within fixed effects as appropriate. In several experiments, the death or failure to flower of one or more plants led to unbalanced sample sizes. In these cases the affected sibship was dropped from the analysis to maintain balanced sampled sizes. The sample sizes reported in Table 1 are the actual sample sizes used in the analyses.

Interpretation of the overall ANOVA's for most experiments was hampered by violation of assumptions (homogeneity of variances and normality of residuals), even after data transformation. Different approaches were taken to address these problems. We analysed position in a separate set of two-way ANOVA's in which position and plant were used as main effects. In several experiments, we calculated an average flower number or average proportion of ray flowers over all heads at one position or over all the heads on a plant. Use of these average values as dependent variables dramatically improved the consistency of the data with the assumptions of ANOVA.

RESULTS

EFFECTS OF DATE

Date had significant effects on both the number of flowers per head and the proportion of ray flowers in all four species examined, according to one way ANOVA's. The patterns of change were well-described by linear regression models, which accounted for 67–88% of the variation in the average proportion of ray flowers and 90–96% of the variation in average flower number per head in the different species. The proportion of ray flowers increased and the flower number per head declined over the blooming period (Fig. 2). The flower number per head declined by 14–28% over the blooming period and the proportion of ray flowers increased by a more modest 3–16% over the same period. (These percentage differences and others reported in this paper are calculated by dividing the difference by the smaller value and multiplying by 100.)

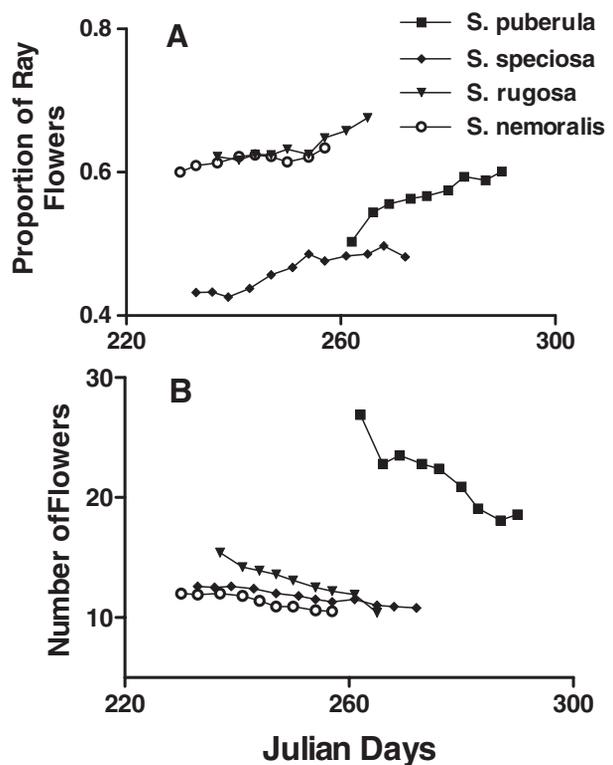


Figure 2. Changes in the proportion of ray flowers (A) and number of flowers per head (B) with date in four species of goldenrod.

EFFECTS OF POSITION

A total of ten experiments examined effects of position. For the two species in which heads were examined at five positions, there was no significant effect on the proportion of ray flowers in *S. caesia*, and a slight but significant tendency for a higher proportion of ray flowers towards the base of the inflorescence in *S. puberula*, with 53% ray flowers in the tip heads and 57% ray flowers in heads on the lowest branch in the inflorescence. In the remaining eight experiments, comparisons involved only two positions, the stem tip and lowest branch, and in six of these experiments, involving four species, position had a significant effect on the proportion of ray flowers (Fig. 3). In each case, the percentage of ray flowers in branch heads exceeded that in tip heads, though the differences were modest, ranging from 3% to 17%. Variation among plants within an experiment was considerable, with a significant added variance component due to plant in every experiment. Furthermore, the plant-position interaction was significant in nine of the ten experiments. Thus the differences due to position were small and somewhat variable among individuals within an experiment.

Effects of position on the numbers of flowers per head were also slight, but often significant. Tip heads had significantly more flowers than branch heads in five of the eight experiments (four of five species) involving a comparison of tip and branch heads (Fig. 4), and in an eighth experiment the probability was 0.08. There was also significant variation among positions in the two experiments examining heads at five positions, and tip heads had the most flowers in both experiments. In the seven experiments producing significant results, the number of flowers in tip heads exceeded that in branch heads by an average of 12%. Even so, there was a significant plant–position interaction in nine experiments and a significant added variance component due to plant in all ten experiments. Thus the extent of the position effect varied among plants within experiments.

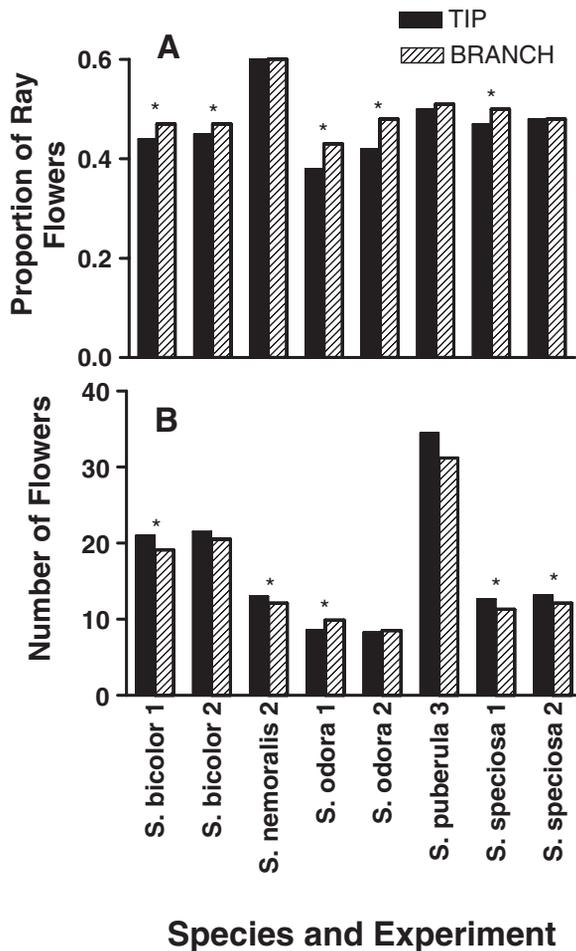


Figure 3. Proportion of ray flowers (A) and number of flowers per head (B) at the inflorescence tip and on the lowest inflorescence branch in five species of goldenrod. Asterisks denote significant differences.

EFFECTS OF ENVIRONMENTAL VARIABLES

The different levels of light, nutrients and water used in our experiments were sufficient to produce visible effects on plant growth, indicating that they were physiologically detectable to the plants. Plants in low light conditions were typically taller, less bushy and had fewer heads. Plants in the low nutrient treatments were smaller than those in high nutrient treatments, bore fewer heads, and often produced foliage that was lighter green.

Of the three environmental variables examined, light and water did not have a significant effect on the proportion of ray flowers in any experiment (Table 2). Nutrient level had a significant effect on the proportion of ray flowers in four of nine experiments (three of five species) and in each case the proportion of ray flowers was higher in the low nutrient treatment. However, the magnitude of these differences was small, ranging from 2% to 7%, and the patterns in the remaining five experiments were inconsistent, with a greater mean in the high nutrient treatment in three cases (Fig. 4).

Effects of environmental variables on the number of flowers per head were also small, with significant differences in only one of five experiments involving light, two of eight experiments involving nutrients, and none of three experiments involving water (Table 3). Of the significant results, heads in the high light treatment of the first *S. bicolor* experiment and in the high nutrient treatment of the second

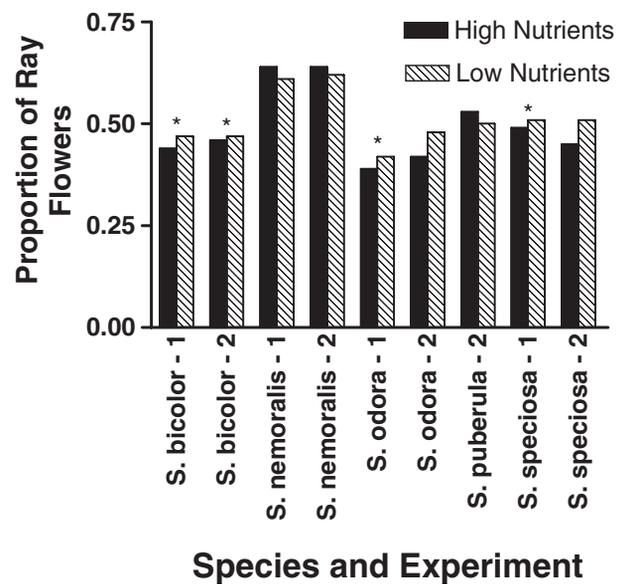


Figure 4. Effect of high and low nutrient levels on the proportion of ray flowers in five species of goldenrod. Asterisks denote significant differences.

Table 2. Results of analyses of variance examining effects of head position and environmental variables on the proportion of ray flowers in heads of five species of *Solidago*

Species and experiment number	Significance of effects						Significant interactions
	Light	Nutrients	Water	Position	Sibship	Plant	
<i>S. bicolor</i> , 1††	NS	*	–	NS	–	–	None
<i>S. bicolor</i> , 2	NS	*	–	NS	NS	***	Pl × Pos**
<i>S. caesia</i> ††	NS	–	–	NS	***	–	S × L***
<i>S. nemoralis</i> , 1	–	NS	–	–	NS	**	None
<i>S. nemoralis</i> , 2†	–	NS	–	–	–	–	None
<i>S. odora</i> , 1†	–	*	NS	–	NS	–	None
<i>S. odora</i> , 2	–	NS	NS	*	NS	***	Pl × Pos***
<i>S. puberula</i> , 1	–	–	–	***	–	***	None
<i>S. puberula</i> , 2†	NS	NS	–	–	NS	–	None
<i>S. puberula</i> , 3	–	–	–	*	–	***	Pl × Pos***
<i>S. speciosa</i> , 1†	–	*	NS	–	–	–	None
<i>S. speciosa</i> , 2	NS	NS	–	NS	NS	***	none

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, NS = not significant; – = not evaluated.

†Denotes analyses in which average value for all heads on a plant was used as dependent variable.

††Denotes analyses in which average values for all heads at a position was used as a dependent variable.

Table 3. Results of analyses of variance examining effects of head position and environmental variables on the number of flowers per head in five species of *Solidago*

Species and experiment number	Significance of effects						Significant interactions
	Light	Nutrients	Water	Position	Sibship	Plant	
<i>S. bicolor</i> , 1††	*	NS	–	*	–	–	None
<i>S. bicolor</i> , 2†	NS	NS	–	–	***	–	None
<i>S. caesia</i> ††	NS	–	–	**	***	–	S × L**
<i>S. nemoralis</i> , 1	–	NS	–	–	*	***	None
<i>S. nemoralis</i> , 2†	–	*	–	–	–	–	–
<i>S. odora</i> , 1†	–	NS	NS	–	*	–	N × W*
<i>S. odora</i> , 2	–	NS	NS	–	NS	***	Pl × Pos***
<i>S. puberula</i> , 1	–	–	–	**	–	***	None
<i>S. puberula</i> , 2†	NS	NS	–	–	NS	–	None
<i>S. puberula</i> , 3	–	–	–	NS	–	***	Pl × Pos***
<i>S. speciosa</i> , 1†	–	*	NS	–	–	–	None
<i>S. speciosa</i> , 2	NS	NS	–	NS	NS	***	Pl × Pos*

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, NS = not significant; – = not evaluated.

†Denotes analyses in which average value for all heads on a plant was used as dependent variable.

††Denotes analyses in which average values for all heads at a position was used as a dependent variable.

S. nemoralis experiment had slightly more flowers than in the respective low resource treatments, but the reverse was true in the first *S. speciosa* experiment.

In contrast to the few and minor effects involving environmental variables, variation among plants and among sibships was often considerable. A significant variance component was associated with plant in

every analysis in which it was a variable, both for the proportion of ray flowers and the number of flowers per head. Sibship accounted for significant variation in the number of flowers per head in four of seven experiments and in the proportion of ray flowers in one of seven experiments. In addition, sibship, plant and position were involved in significant interaction terms in the analyses of several experiments, includ-

ing those reported in Tables 2 and 3, and in preliminary analyses conducted before using average values as dependent variables. The presence of these significant interaction terms means that any effects of environmental variables vary at different positions within a plant, among plants and among sibships, providing further evidence of the lack of consistent environmental effects on the proportion of ray flowers and the number of flowers per head.

DISCUSSION

Our results provide little evidence to support the hypothesis that the presence of two flower types in goldenrods is advantageous in permitting flexible allocation of resources to male and female reproductive functions. The proportion of ray flowers increased slightly over the blooming season, and towards the tip of the inflorescence. However, most experiments involving environmental variables caused no significant changes in floral ratios, and interactions involving plant identity were common, indicating that the patterns that did occur varied among individuals. Only the experiments involving nutrient levels produced significant results, and just in four of nine experiments, with differences of only a few percentage points between the means. Several other studies of diclinous composites have also revealed floral ratios that were relatively invariant in the face of environmental variation, including work with *Cotula* spp. (Lloyd, 1972b), *Iva xanthifolia* (Freeman *et al.*, 1981), *Ambrosia artemisiifolia* (McKone & Tonkyn, 1986; Traveset, 1992) and *Aster* spp. (Bertin & Kerwin, 1998).

The female function is often emphasized under conditions of high resource availability (Cid-Benevento, 1987; Solomon, 1989; Emms, 1993), presumably due to the greater resource needs of the female function than the male function as a result of fruit and seed production (Lloyd, 1980; Traveset, 1992). The few patterns found in our study are not, however, consistent with this explanation. Production of ray flowers was greater in the low nutrient treatment than in the high nutrient treatment in the four experiments showing a significant difference. Additionally, the proportion of ray flowers increased towards the end of the season. In contrast, the numbers of flowers per head declined during the season, presumably reflecting a decline in resource levels as days became shorter and many resources had already been used for flowers and seeds.

The absence of environmental influences on floral ratios in goldenrods does not necessarily prevent these plants from responding to changing environmental conditions by changing sex allocation. Apart from changes in floral ratios, plants can alter sex allocation by changing the production of ovules and anthers per

flower, the number of pollen grains per anther, and the extent of ovule abortion (Mazer, 1992; Delesalle & Mazer, 1996). Of these mechanisms, the number of ovules per goldenrod flower is invariant at one and the number of anthers is also constant. Thus pollen production per anther and ovule abortion are the remaining possible means of regulating sex expression.

The limited variation in floral ratios observed in our experiments could reflect allometric changes. Goldenrod heads are roughly disc-shaped, with ray flowers occupying the circumference of the circle and disc flowers occupying the centre. Because the area of the disc surface (i.e. the space occupied by disc flowers) increases faster than the circumference as the radius of the disc increases, the proportion of ray flowers should decline as disc (head) size increases. While we did not measure the radius of the goldenrod heads (and such measurements would be difficult to make with accuracy and precision), the total number of flowers per head can be used as a rough measure of head size. Using this measure, we note that the proportion of ray flowers increased over the blooming season as flower number decreased (Fig. 2). Similarly, heads at the inflorescence tip tended to have more flowers and a lower proportion of ray flowers than heads on lower branches. Finally, in the three experiments where numbers of flowers differed significantly between high and low resource treatments, high flower numbers were associated with a low proportion of ray flowers in each case. Thus, even though the lack of measurements of head size precludes a formal allometric analysis, the patterns observed are consistent with an allometric interpretation of at least some of the variation in proportions of the two flower types.

There are few other studies of gynomonoeious taxa. Lloyd & Bawa (1984) reported unpublished work on two gynomonoeious species, *Gunnera insignis* and *Artemisia vulgaris*. The former showed considerable variation in the percentage of female flowers, while sex expression varied little in the latter species, although the effects of particular environmental variables were not studied. Bertin & Kerwin (1998) examined 16 gynomonoeious species of *Aster* but found no consistent effects on floral ratios of date, plant size, nutrient availability, light intensity or position of heads on the plant.

The present study showed frequent variation among plants and among sibships in both the proportion of ray flowers and the number of flowers per head. Similar differences were observed in the same variables in *Aster* (Bertin & Kerwin, 1998) and in seed-ovule ratios in another composite, *Achillea ptarmica* (Andersson, 1993). Such variation seems surprising in view of the constancy of many of these parameters in the face of environmental variation. Andersson (1993) suggested that the considerable among-plant variation in seed/

ovule ratio, a trait expected to be closely related to fitness, could reflect genetic load generated by sexual reproduction in this outcrossing species, coupled with the maintenance of less reproductively fit genotypes by extensive clonal propagation. While ratios of flower types may be less directly connected to plant fitness than seed/ovule ratios, similar forces could underlie the variation observed in asters and goldenrods. Both groups are highly outcrossed and some species propagate clonally (Jones, 1978; Gross & Werner, 1983).

If flexibility in sex allocation has not been important in the evolution and maintenance of gynodioecy in goldenrods, what are the selective advantages of this sexual system? Bertin & Kerwin (1998) summarized four other explanations: enhancement of pollinator attraction, reduction in inbreeding depression, reduction in pollen–pistil interference and lower rates of floral predation.

Many aspects of plant reproductive biology have been interpreted as advantageous in reducing the negative consequences of inbreeding depression. In goldenrods and other gynodioecious species, the presence of female ray flowers in combination with interfloral protogyny causes the stigmas of these flowers to be displayed before pollen is released from disc flowers in the same head. This arrangement could reduce the frequency of self-pollination and therefore the proportion of progeny that result from self-fertilization (Lloyd, 1972a,b; Burt, 1977; Willson, 1983). However, goldenrods apparently are physiologically self-incompatible (Mulligan & Findlay, 1970; Gross & Werner, 1983), meaning that self-fertilization would not occur even after self-pollination, making gynodioecy irrelevant as a mechanism to reduce inbreeding.

Self-pollination could be problematic in other ways, however, even in self-incompatible species (Lloyd & Yates, 1982). Male fitness could be reduced because deposition of self-pollen reduces the quantity of pollen available for export and therefore the opportunities for siring offspring on other plants. Female fitness could also suffer if self-pollen interferes in some way with the success of pollen arriving from other plants. The possibility of such pollen–pistil interference has not been explored in goldenrods, although there is evidence of its occurrence in other species (Waser & Price, 1991; Dinné, 1997).

Another possibility is that the presence of female ray flowers is unrelated to selection for femaleness, and instead reflects selection for the presence of conspicuous rays (petals) for pollinator attraction (Leppik, 1977; Marshall & Abbott, 1984; Abbott & Schmitt, 1985). Such an argument assumes that rays and stamens are alternate developmental states, a condition that has been demonstrated in another composite, *Senecio squalidus* (Ingram & Taylor, 1982).

However, many other family members (Liguliflorae) possess bisexual, ligulate flowers, i.e. ones that bear both a ray and a functional androecium.

A fourth possibility is that unisexual female flowers result from selection to separate at least some of the ovules from tissues that are attractive to herbivores. As Burt (1977) has noted, a composite head ‘offers a well stocked larder’ to herbivorous insects. If some of these insects specialize on pollen, but cause incidental damage to the ovules of bisexual flowers, it is advantageous to produce at least some pistils in flowers that lack pollen.

In conclusion, we do not believe that gynodioecy in goldenrods is advantageous in permitting flexibility in allocation of resources to male and female functions. Rather, as has been suggested for the genus *Aster*, we think that promotion of floral attractiveness and avoidance of pollen–pistil interference are more likely explanations for the evolution of this trait. These hypotheses are both amenable to experimental evaluation.

ACKNOWLEDGEMENTS

We thank Ken Prestwich, Susan J. Mazer and an anonymous referee for helpful comments on an earlier draft of the manuscript. Financial support was provided by College of the Holy Cross and the Sherman Fairchild Foundation.

REFERENCES

- Abbott RJ, Schmitt J. 1985.** Effect of environment on percentage female ray florets per capitulum and outcrossing potential in a self-compatible composite (*Senecio vulgaris* L. var. *hibernicus* Syme). *New Phytologist* **101**: 219–229.
- Ackerly DD, Jasienski M. 1990.** Size-dependent variation of gender in high density stands of the monoecious annual, *Ambrosia artemisiifolia* (Asteraceae). *Oecologia* **82**: 474–477.
- Andersson S. 1993.** The potential for selective seed maturation in *Achillea ptarmica* (Asteraceae). *Oikos* **66**: 36–42.
- Barker PA, Freeman DC, Harper KT. 1982.** Variation in the breeding system of *Acer grandidentatum*. *Forest Science* **28**: 563–572.
- Bateman AJ. 1948.** Intra-sexual selection in *Drosophila*. *Heredity* **2**: 349–368.
- Bertin RI. 1982.** The ecology of sex expression in red buckeye. *Ecology* **63**: 445–456.
- Bertin RI, Kerwin MA. 1998.** Floral sex ratios and gynodioecy in *Aster* (Asteraceae). *American Journal of Botany* **85**: 235–244.
- Bierzuchudek P. 1984.** Determinants of gender in Jack-in-the-pulpit: the influence of plant size and reproductive history. *Oecologia* **65**: 14–18.
- Burt BL. 1977.** Aspects of diversification in the capitulum. In: Heywood VH, Harborne JB, Turner BL, eds. *The biology and*

- chemistry of the Compositae, Vol. I. London: Academic Press, 41–59.
- Charnov EL, Bull J. 1977.** When is sex environmentally determined? *Nature* **266**: 828–830.
- Cid-Benevento CR. 1987.** Relative effects of light, soil moisture availability and vegetative size on sex ratio of two monoecious woodland annual herbs: *Acalypha rhomboidea* (Euphorbiaceae) and *Pilea pumila* (Urticaceae). *Bulletin of the Torrey Botanical Club* **114**: 293–306.
- Coleman JR, Coleman MA. 1982.** Reproductive biology of an andromonoecious *Solanum* (*S. palinacanthum* Dunal). *Biotropica* **14**: 69–75.
- Dawson TE, Ehleringer JR. 1993.** Gender-specific physiology, carbon isotope discrimination, and habitat distribution in boxelder, *Acer negundo*. *Ecology* **74**: 798–815.
- Delesalle VA, Mazer SJ. 1996.** Nutrient levels and salinity affect gender and floral traits in the autogamous *Spergularia marina*. *International Journal of Plant Sciences* **157**: 621–631.
- Diggle PK. 1991.** Labile sex expression in andromonoecious *Solanum hirtum*: pattern of variation in floral structure. *Canadian Journal of Botany* **69**: 2033–2043.
- Dinnézt P. 1997.** Male sterility, protogyny, and pollen-pistil interference in *Plantago maritima* (Plantaginaceae), a wind-pollinated, self-incompatible perennial. *American Journal of Botany* **84**: 1588–1594.
- Emms SK. 1993.** Andromonoecy in *Zigadenus paniculatus* (Liliaceae): spatial and temporal patterns of sex allocation. *American Journal of Botany* **80**: 914–923.
- Freeman DC, Klikoff LG, Harper KT. 1976.** Differential resource utilization by the sexes of dioecious plants. *Science* **193**: 597–599.
- Freeman DC, MacArthur ED, Harper KT, Blauer AC. 1981.** Influence of environment on the floral sex ratio of monoecious plants. *Evolution* **35**: 194–197.
- Gregg KB. 1975.** The effect of light intensity on sex expression in species of *Cynoches* and *Catasetum* (Orchidaceae). *Selbyana* **1**: 101–113.
- Gregg KB. 1978.** The interaction of light intensity, plant size, and nutrition in sex expression in *Cynoches* (Orchidaceae). *Selbyana* **2**: 212–223.
- Gross RS, Werner PA. 1983.** Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). *Ecological Monographs* **53**: 95–117.
- Ingram R, Taylor L. 1982.** The genetic control of a non-radiate condition in *Senecio squalidus* L. and some observations on the role of ray florets in the Compositae. *New Phytologist* **91**: 749–756.
- Janzen DH. 1977.** A note on optimal mate selection by plants. *American Naturalist* **111**: 365–371.
- Jones AG. 1978.** Observations on reproduction and phenology in some perennial asters. *American Midland Naturalist* **99**: 184–197.
- Leppik EE. 1977.** The evolution of capitulum types of the Compositae in the light of insect–flower interaction. In: Heywood VH, Harborne JB, Turner BL, eds. *The biology and chemistry of the Compositae*, Vol. I. London: Academic Press, 61–89.
- Lloyd DG. 1972a.** Breeding systems in *Cotula* L. (Compositae, Anthemideae) I. The array of monoclinal and diclinal systems. *New Phytologist* **71**: 1181–1194.
- Lloyd DG. 1972b.** Breeding systems in *Cotula* L. (Compositae, Anthemideae). *New Phytologist* **71**: 1195–1202.
- Lloyd DG. 1980.** Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytologist* **86**: 69–79.
- Lloyd DG, Bawa KS. 1984.** Modification of the gender of seed plants in varying conditions. *Evolutionary Biology* **6**: 255–338.
- Lloyd DG, Webb CJ, Primack RB. 1980.** Sexual strategies in plants. II. Data on temporal regulation of maternal investment. *New Phytologist* **86**: 81–92.
- Lloyd DG, Yates JMA. 1982.** Intrasexual selection and the segregation of pollen and stigmas in hermaphrodite plants, exemplified by *Wahlenbergia albomarginata* (Campanulaceae). *Evolution* **36**: 903–913.
- Lovett Doust J. 1980.** Floral sex ratios in andromonoecious Umbelliferae. *New Phytologist* **85**: 265–273.
- Lovett Doust J, Harper JL. 1980.** The resource costs of gender and maternal support in an andromonoecious umbellifer, *Smyrniolum olusatrum* L. *New Phytologist* **85**: 251–264.
- Mabberly DJ. 1997.** *The plant-book*. Cambridge: Cambridge University Press.
- Marshall DF, Abbott RJ. 1984.** Polymorphism for outcrossing frequency at the ray floret locus in *Senecio vulgaris* L. III. Causes. *Heredity* **53**: 145–149.
- May PG, Spears EE Jr. 1988.** Andromonoecy and variation in phenotypic gender of *Passiflora incarnata* (Passifloraceae). *American Journal of Botany* **75**: 1830–1841.
- Mazer SJ. 1992.** Environmental and genetic sources of variation in floral traits and phenotypic gender in wild radish: consequences for natural selection. In: Wyatt R, ed. *Ecology and evolution of plant reproduction: new approaches*. New York: Chapman & Hall, 281–325.
- McKone MJ, Tonkyn DW. 1986.** Intrapopulation gender variation in common ragweed (Asteraceae: *Ambrosia artemisiifolia* L.), a monoecious, annual herb. *Oecologia* **70**: 63–67.
- Méndez M. 1998.** Modification of phenotypic and functional gender in the monoecious *Arum italicum* (Araceae). *American Journal of Botany* **85**: 225–234.
- Méndez M. 2001.** Sexual mass allocation in species with inflorescences as pollination units: a comparison between *Arum italicum* and *Arisaema* (Araceae). *American Journal of Botany* **88**: 1781–1785.
- Mossop R, Macnair MR, Robertson AW. 1994.** Within-population variation in sexual resource allocation in *Mimulus guttatus*. *Functional Ecology* **8**: 410–418.
- Müller H. 1883.** *The fertilisation of flowers*. London: MacMillan. (English translation by D.W. Thompson).
- Mulligan GA, Findlay JN. 1970.** Reproductive systems and colonization in Canadian weeds. *Canadian Journal of Botany* **48**: 859–860.

- Primack RB, Lloyd DG. 1980.** Andromonoecy in the New Zealand montane shrub manuka, *Leptospermum scoparium* (Myrtaceae). *American Journal of Botany* **67**: 361–368.
- Richards AJ. 1986.** *Plant breeding systems*. London: George Allen & Unwin.
- Schlessman MA. 1982.** Expression of andromonoecy and pollination of tuberous lomatiums (Umbelliferae). *Systematic Botany* **7**: 134–149.
- Solomon BP. 1985.** Environmentally influenced changes in sex expression in an andromonoecious plant. *Ecology* **66**: 1321–1332.
- Solomon BP. 1989.** Size-dependent sex ratios in the monoecious, wind-pollinated annual, *Xanthium strumarium*. *American Midland Naturalist* **121**: 209–218.
- Stromberg JC, Patten DT. 1990.** Flower production and floral ratios of a southwestern riparian tree, Arizona walnut (*Juglans major*). *American Midland Naturalist* **124**: 278–288.
- Traveset A. 1992.** Sex expression in a natural population of the monoecious annual, *Ambrosia artemisiifolia* (Asteraceae). *American Midland Naturalist* **127**: 309–315.
- Waser NM, Price MV. 1991.** Reproductive costs of self-pollination in *Ipomopsis aggregata* (Polemoniaceae): are ovules usurped? *American Journal of Botany* **78**: 1036–1043.
- Willson MF. 1983.** *Plant Reproductive Ecology*. New York: John Wiley and Sons.
- Willson MF, Ruppel KP. 1984.** Resource allocation and floral sex ratios in *Zizania aquatica*. *Canadian Journal of Botany* **62**: 799–805.
- Yampolsky C, Yampolsky H. 1922.** Distribution of sex forms in the phanerogamic flora. *Bibliotheca Genetica* **3**: 1–62.