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COMPONENTS OF REPRODUCTIVE EFFORT AND YIELD IN GOLDENRODS[1]

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ABSTRACT

Four components of reproductive yield (the weight of reproductive tissue) were examined in relation to their effect on reproductive effort and their relative contributions to reproductive yield in five species of goldenrods (*Solidago,* Compositae). The yield components were number of flowing stems per plant, number of flowering branches per stem, number of flowering heads per branch, and number of seeds per seed head. Individuals within populations increase their reproductive effort by increasing their reproductive weight, not by decreasing their vegetative weight. Each species shows a different pattern of positive correlations of yield components with reproductive yield and reproductive effort, indicating that each species has its own mechanisms for regulating reproduction. The yield components were not significantly intercorrelated.

LIFE HISTORY THEORY predicts that organisms utilize their available resources for growth, maintenance, and reproduction in a manner which maximizes fitness (Stearns, 1977). Theoretical and empirical treatments of plant growth form and habitat stability have shown that plants can distribute stem, leaf, and reproductive tissue biomass such that individual fitness is maximized (Abrahamson and Gadgil, 1973; Gadgil and Solbrig, 1972; Grime, 1977; Primack, 1979; Schaffer and Gadgil, 1975). In such empirical studies, reproductive effort (the percentage of plant weight which is reproductive tissue) and reproductive yield (the total weight of reproductive tissue produced) are generally treated as single variables. However, variation in reproductive yield can be partitioned into separate components which together determine the total reproductive yield of a plant. In crop plants, yield components are often negatively correlated (Adams, 1967; Grafius and Thomas, 1971). Only a few studies have examined the correlations among reproductive yield components in natural populations (Salisbury, 1942; Werner and Platt, 1976; Wilbur, 1976; Willson and Price, 1977; Primack, 1978) and these have not considered the relationship of yield components to such variables as reproductive effort. The purpose of this present study is to contrast reproductive yield and reproductive effort in five species of herbaceous, perennial goldenrods (*Solidago,* Compositae) and to examine how individuals

of these species differ in their ability to regulate reproductive yield and reproductive effort through variation in four yield components: the number of flowering stems per plant, the number of flowering branches per flowering stem, the number of heads per flowering branch, and the number of seeds per head.

MATERIALS AND METHODS—Twenty plants of each of five species of goldenrods were collected from the Hammond Woods, Newton, Middlesex County, Massachusetts in September and October 1979, when the seeds were fully mature. Species came from open disturbed ground, (*S. canadensis* L. and *S. juncea* Ait.); from the edge of a forest (*S. puberula* Nutt. and *S. odora* Ait.), and from the interior of a forest (*S. caesia* L.). Plants were collected over an area of approximately 100 m² to minimize the chances that two plants came from the same clone. Each specimen was a single above-ground shoot. Plants were cut at ground level, oven dried for 72 hr at 70 C, and then evaluated in the laboratory for the following characters:

Yield components: a) Number of flowering stems (St) per plant. b) Number of flowering branches (Br) per flowering stem; data taken from the flowering shoot median in length. c) Number of mature seed heads (Hd) per flowering branch; data taken from the flowering branch median in length. d) Number of seeds (Sd) per mature seed head; a mean value based on a sample of three seed heads per plant.

Weight of parts: e) Weight of all leaves (living and dead). f) Weight of stems. g) Weight of reproductive tissue (seed heads).
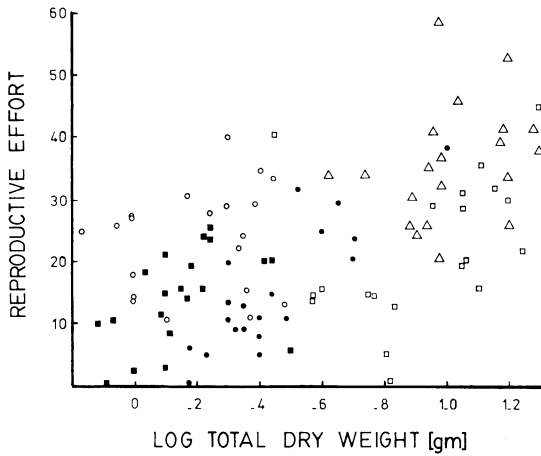
Fig. 1. Reproductive effort (percentage of total dry weight of a plant which is reproductive weight) and the log of the total dry weight for goldenrod plants collected from open disturbed ground, *Solidago canadensis* (open squares) and *S. juncea* (open triangles); forest edge, *S. puberula* (open circles) and *S. odora* (closed circles); and forest interior, *S. caesia* (closed squares).

Reproductive effort was calculated as the percentage of total weight which was reproductive tissue. This analysis did not consider below-ground tissue. All statistical comparisons of group means were done using one-way analyses of variance (ANOVA). All correlations presented are Pearson product-moment correlations.

RESULTS—The five species were significantly different ($P < 0.05$; one-way ANOVA) in their mean values for all seven characters measured and reproductive effort (Table 1). The forest species, *S. caesia*, had the lowest reproductive effort, and a species of open

ground, *S. juncea*, had the highest reproductive effort. The species inhabiting edge habitats had intermediate values for reproductive effort and total weight (Fig. 1).

Variation in reproductive effort within species is not consistently correlated with leaf weight or stem weight (Table 2) but shows a strong positive correlation with reproductive weight in all five species. This suggests that individual plants of these species, except *S. odora*, have a high reproductive effort because they have more reproductive tissue but not because they have more or less leaf or stem tissue. Flowering stem number per plant was not correlated with reproductive effort in any species. However, reproductive effort was positively correlated with the number of flowering branches per stem and head number per branch in two species each, and seed number per head in one species. The four yield components were not correlated with reproductive effort in *S. puberula* and *S. juncea*, indicating that individuals of these species are less able to alter their reproductive effort through variation in yield components.

Reproductive weight shows very different patterns of correlation with yield components in each species (Table 3). Only in *S. caesia* is the number of flowering stems per plant correlated with reproductive weight, while only in *S. canadensis* is seed number per head correlated with yield. Individuals of each species are capable of increasing their reproductive weight through variation in one or two yield components and most species have unique combinations of yield components which regulate the reproductive weight. All of the significant correlations between yield components and reproductive weight were positive.

The yield components were not strongly cor-

TABLE 1. *Components of reproductive effort and yield in goldenrods. Mean and standard deviations for 20 plants each of five goldenrod species. Species arranged in order of increasing reproductive effort (RE). Habitats are woods (W), edge of woods (E), and open disturbed field (F). Units are percentages for reproductive effort, numbers for yield components, and $g \times 10^2$ for the weights*

Species	Habitat	RE	Reproductive Yield Components				Weight		
			Stems	Branches	Heads	Seeds	Leaves	Stems	Reproductive
S. caesia	W	15 ± 7	1.5 ± 1.0	9 ± 5	5 ± 1	7 ± 2	69 ± 26	61 ± 26	24 ± 16
S. odora	E	16 ± 10	1.0 ± 0.0	11 ± 6	28 ± 24	7 ± 1	122 ± 44	134 ± 92	67 ± 96
S. canadensis	F	22 ± 11	3.3 ± 3.5	21 ± 10	33 ± 30	16 ± 4	282 ± 131	450 ± 205	251 ± 231
S. puberula	E	24 ± 8	1.6 ± 0.9	20 ± 7	3 ± 1	19 ± 3	47 ± 29	84 ± 33	43 ± 26
S. juncea	F	36 ± 10	1.0 ± 0.2	16 ± 6	64 ± 23	12 ± 4	229 ± 84	469 ± 179	415 ± 215
ANOVA F[a]		16.5[b]	6.3	12.1	30.9	66.2	37.4	48.6	26.0

[a] The F values result from one-way ANOVA tests of the null hypothesis that species means are equal for each variable examined ($P < 0.001$).

[b] Data arcsine transformed for ANOVA test.

TABLE 2. *Components of reproductive effort and yield in goldenrods. Correlation coefficients of reproductive effort with reproductive yield components and weights in five goldenrod species*

Species	Reproductive yield components				Weight		
	Stems	Branches	Heads	Seeds	Leaves	Stem	Reproductive
S. caesia	0.27	0.66[b]	0.29	0.31	0.14	0.03	0.85[b]
S. odora	0.00	0.94[b]	0.85[b]	0.21	0.49[a]	0.76[b]	0.82[b]
S. canadensis	0.06	0.22	0.49[a]	0.59[b]	0.22	0.35	0.79[b]
S. puberula	0.17	0.16	0.38	0.13	−0.22	0.06	0.75[b]
S. juncea	−0.10	0.11	0.23	0.24	−0.08	−0.09	0.71[c]

[a] $P < 0.05$.
[b] $P < 0.01$.
[c] $P < 0.001$.

related among themselves (Table 4). However, in *S. odora,* the number of branches per flowering stem was positively correlated with the number of heads per flowering branch.

DISCUSSION—Reproductive effort is a complex biological variable which is a product of many processes within a plant. Theoretically, an individual plant could show increased reproductive effort either by *increasing* its reproductive yield (with vegetative size held constant), by *decreasing* its vegetative weight (with reproductive yield held constant), or both simultaneously. This study has shown that within populations of four of the goldenrod species, individuals increase their reproductive effort through increasing reproductive

TABLE 3. *Components of reproductive effort and yields in goldenrods. Correlation coefficients of reproductive weight with yield components in five goldenrod species*

Species	Reproductive yield components			
	Stems	Branches	Heads	Seeds
S. caesia	0.59[b]	0.57[b]	0.22	0.13
S. odora	0.00	0.80[b]	0.76[b]	0.19
S. canadensis	0.37	0.28	0.34	0.52[a]
S. puberula	0.01	0.29	0.58[b]	0.29
S. juncea	−0.13	0.37	0.56[b]	−0.11

[a] $P < 0.05$.
[b] $P < 0.01$.

yield, with vegetative weight remaining relatively constant. In *S. odora,* individuals increase their reproductive effort both through higher reproductive yields and larger vegetative size. The yield components which allow individuals to increase their reproductive effort are typically branch number per flowering stem, head number per branch, and seed number per head. The number of flowering stems is presumably not as responsive to changes in the physiological status of the plant.

Reproductive yield is regulated by different components in each of these species. Despite a general superficial resemblance in growth form and inflorescence architecture, each species has a distinctive mechanism for controlling the final reproductive yield. For example, only mean seed number per head was correlated with yield in *S. canadensis,* while both the number of flowering stems per plant and the number of branches per flowering stem were correlated with yield in *S. caesia.* Within each species, these yield components vary independently of one another as in species of milkweeds (Wilbur, 1976), unlike many crop species which show negative correlations among reproductive yield components (Adams, 1967) and unlike many natural populations in which the correlations are positive (Primack, 1978).

Abrahamson and Gadgil (1973) hypothesized that the reproductive effort of a species is, in part, dependent on habitat characteristics.

TABLE 4. *Components of reproductive effort and yield in goldenrods. Correlation coefficients among yield components in five goldenrod species. Abbreviations for yield components are given in the text*

Species	St × Br	St × Hd	St × Sd	Br × Hd	Br × Sd	Hd × Sd
S. caesia	0.06	−0.14	0.11	−0.06	−0.01	0.25
S. odora	0.00	0.00	0.00	0.81[a]	0.25	0.12
S. canadensis	0.02	−0.29	−0.11	0.22	0.05	0.43
S. puberula	−0.41	0.02	−0.11	0.23	−0.07	0.11
S. juncea	−0.15	−0.32	0.33	0.16	−0.32	−0.42

[a] $P < 0.001$.

Species occupying short-lived habitats should tend to be "r" selected (Gadgil and Solbrig, 1972) and allocate a substantial portion of the total plant biomass to reproductive tissues. Conversely, species occupying stable habitats should be "K" strategists and allocate plant biomass to maintenance tissues. Data on growth form of four species of *Solidago* presented by Abrahamson and Gadgil (1973) and the results of this study (Fig. 1) support these predictions. The habitat of *S. caesia* is the most stable of the three habitats examined, yet the most light stressed. As we would predict, this species had a low reproductive effort and allocated the highest proportion of biomass to leaf tissue (45%) of the five species. Field habitats are often characterized by a high degree of disturbance and competition for light by similar growth form taxa (Abrahamson and Gadgil, 1973; Grime, 1977). In this environment, selection would favor high reproductive effort and increasing height to elevate leaves above potential light competitors. Our field species, *S. juncea* and *S. canadensis,* were the tallest of the five species and had high reproductive effort values. The edge habitat species, *S. puberula* and *S. odora,* occupy an intermediate habitat with respect to disturbance and their reproductive effort values were intermediate between the extremes of the *S. caesia* (woods) and *S. juncea* (field).

In conclusion, goldenrod species have differences in reproductive effort which can be related to the environments which they occupy. The variation in reproductive effort within each species can be further partitioned into a series of reproductive components. This type of investigation reveals that individuals of each of these related goldenrod species has distinct mechanisms for regulating reproductive yield, and consequently reproductive effort. A logical further step in this inquiry would be to learn why a species utilizes particular mechanisms, and not others, for regulating reproductive effort.

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