Adaptive Significance of Ray Corollas in Helianthus grosseserratus (Compositae)

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ABSTRACT: A major concern in plant evolution is to what extent morphological features are adaptive. Determining the value of a particular character state requires: (1) an hypothesis for the function of the character, and (2) a prediction and suitable test. An example of this approach in Compositae deals with ray corollas of *Helianthus grosseserratus*. Because the ray florets are neuter (*i.e.*, do not set seed), the hypothesis is that the corollas function to attract pollinators to the disc florets. If the rays are removed, then fewer pollinators should be attracted. The prediction was tested in control (rayed) and experimental (rayless) populations directly by observing pollinator visits and indirectly by determining seedset. Four seasons of fieldwork have shown that: (1) frequency of visitation of pollinators was 61% lower for rayless populations, and the diversity of pollinators dropped sharply; and (2) seedset in rayless populations was 64% lower than for the rayed population. These data are consistent with the hypothesis that the ray corollas in *H. grosseserratus* serve to attract pollinators and that the structures are adaptive.

INTRODUCTION

Although in a general sense organisms are obviously adapted to their environments, our understanding of the specific ways in which particular structures function for survival and reproductive success is frequently limited, especially in flowering plants. As Van Valen (1973, p. 333) has emphasized: "We should know what characters are, or have been, important to an organism, even for angiosperms, where little research has been directed at the problem. . . ." Some workers have viewed as minimal the adaptive value of many features in angiosperms (*e.g.*, Cronquist, 1969), and others have criticized studies of adaptation in a general sense (Gould and Lewontin, 1979). But still others have responded with positive support for experimental approaches (*e.g.*, Mayr, 1983).

The adaptive value of morphological structures has been studied in various taxa of Compositae, one of the larger families of angiosperms, and these have included investigations on growth form (Abrahamson and Gadgil, 1973), leaves (Smith and Nobel, 1978), fruiting heads and isolated fruits (Zohary, 1950; Leppik, 1960, 1970, 1977; Burtt, 1961, 1977; Burrows, 1973, 1975; Sheldon and Burrows, 1973; Levin and Turner, 1977; Vogel, 1979; Ridley, 1982a, b; and Venable and Levin, 1983), pollen (Blackmore, 1982), pollination mechanisms (Estes and Thorp, 1975), and breeding systems (Ingram and Taylor, 1982; Marshall and Abbott, 1982). But despite these numerous studies which have demonstrated some correlations of morphology with environmental factors, most have not attempted to test hypotheses derived from these correlations. This point has been stressed in a general way for the angiosperms by Ehrendorfer (1973).

A simple focus in Compositae for an experimental approach is on the adaptive value of ray corollas. A reasonable hypothesis is that they serve to attract pollinators to the disc florets. *Helianthus grosseserratus* Martens was selected for study because it has large, conspicuous heads and rays, and shows strong contrast in ultraviolet light (pers. observ.); because the ray florets are neuter and do not themselves set seed; because previous work had shown the species to be self-incompatible (Heiser *et al.*, 1969), and because plants were conveniently accessible. Predictions from the hypothesis are that removal of ray corollas from heads of *H. grosseserratus* will result in lowered reproductive success via fewer pollinators visiting the rayless heads and, consequently, lowered seedset. These predictions can be tested by removing ray corollas from populations of *H. grosseserratus* and comparing the numbers of insect visitors and seedset with control populations.

The purposes of this paper, therefore, are: (1) to indicate the effects of ray corolla removal on insect visitors and seedset in one population of *Helianthus grosseserratus,* and (2) to offer suggestions on the adaptive significance of ray corollas in this species and more generally in the entire family.

MATERIALS AND METHODS

For the experiments, a field 500 m^2 containing *Helianthus grosseserratus* was selected in Columbus, Ohio, on property owned by the Metropolitan Parks Division halfway between Bethel and Henderson Roads and between Olentangy River Road and Rte. 315. This is an old field with small groves of trees and large open areas, some of which have been used for vegetable gardening.

The experimental design in the growing seasons of 1976-1979 established three populations, rayed, rayless, and field, within which individuals were spaced 0.5-1 m apart. In tests of pollinator visits and seedset the rayed population was the control and the rayless population the experimental group. In testing the levels of seedset in the rayed population in contrast to normal field conditions, the rayed population was the experimental group and the field population the control.

The spatial arrangement of the populations was different each year. In 1976 the rayed and rayless plants were intermixed in the same area; in 1977 they were separated by 11.5 m; in 1978 and 1979 they were separated by 50 m. In the latter 2 years the same populations were used for rayed and rayless plants, but they were simply switched (*i.e.,* the population that was rayed in 1978 became rayless in 1979 and vice versa). In all years the field populations were 50 m from the rayed and rayless populations. Further, in the areas between and surrounding (50-m radius) the rayed and rayless populations, all other flowering branches of *Helianthus grosserratus* were removed during the course of the experiments.

All heads except one were removed from each rayed and rayless plant to provide a uniform spatial separation of heads within a population. In the field populations, heads were left as ordinarily found with six or more on each plant. Heads were made rayless by plucking off the ray corollas before anthesis. For all populations, heads were collected at maturity, placed in paper envelopes, labeled and stored in the laboratory for later analysis.

Bagging studies were done in the greenhouse to determine breeding systems as a confirmation of the observation by Heiser *et al.* (1969) that *Helianthus grosseserratus* is self-incompatible. Four individuals from the field population were potted, brought into the OSU greenhouse, bagged, hand-pollinated after anthesis, and measured for seedset. Holding these pots for an additional year served to demonstrate clearly that *H. grosseserratus* is clonal: several new shoots (not seedlings) arose the following year in the same pots even though no seeds were set. In plants with self-incompatible breeding systems, clones will set fewer seed as a result of ineffective lateral pollen flow. Only incoming, compatible new pollen will allow for potentially good seedset. Because it was not known how many clones existed in the rayed and rayless populations, the 1978 experiments were repeated in 1979 using plants from the same areas, but with the rayed being the rayless and vice versa. In this fashion the clonal problem was surmounted without knowing exactly how many clones were present in each population.

Estimates of insect visitors to rayed and rayless populations were made on 13, 15, and 16 September 1979 in the same location. Five heads in the center of each population were simultaneously monitored, and most insect visitors were captured. Ones that escaped were recorded and added to the total insect numbers. All observation days were clear and sunny. Preliminary observations in 1978 showed that most insect activity occurred between 9:00 AM and 3:00 PM, and this was the period of principal sampling in 1979.

RESULTS

Seedset.—The percent of fertile achenes set per head in all of the populations in all years is low (7.2%; Table 1). The mean number of florets per head in each of the populations varied somewhat from year to year (Table 1), but the values were similar for all years for all populations except 1977, when the numbers were lower. The percent fertile achenes per head, however, was not unusually lower than in other years, but both the lowest (1.5%), and highest (15.3%) values were recorded during that year.

One unanticipated problem was interpreting whether or not an achene was fertile. Although this would seem straightforward, the difficulty is with achenes without developed embryos (pseudoachenes; Table 1), which often are full size, correct shape, and have even coloration (although they *tend* to be more uniformly dark in color). Often insect larvae are inside, although sometimes only an exit hole remains. Larvae of several insect groups were found in the pseudoachenes of *Helianthus grosseserratus* (listed in order of abundance): Coleoptera, Curculionidae, *Smicronyx* (over one-half of the 42 collected larvae were of this genus); Diptera, Cecidomyiidae, *Neolasioptera* and *Asphondylia;* Hymenoptera, Torymidae; and Lepidoptera, Cochylidae, *Phalonia.* Some of these insects may oviposit on the young unopened flower buds and develop inside the ovules (Satterthwait, 1946; Oseto and Braness, 1979). In any event, the development of the larvae promotes structural development of the pericarp of the achene so that distinguishing fertile achenes from pseudoachenes must be done carefully by examining every apparently fertile achene. The percent occurrence of pseudoachenes is sufficiently high per head (average 3.6%) to be important in calculating the results. It is possible that these achenes might have been successfully pollinated and become fertile if the destruction by larvae had not occurred, but the appearance of pseudoachenes at very similar levels in the rayed and rayless populations (average 3.0% and 3.2% per head in the 4 years combined) suggests that this did not skew the results.

TABLE 1.—Seedset data for populations of *Helianthus grosseserratus* during the summers of 1976-1979

Year and type of population	Number of heads	Average number florets/ head	Number of fertile achenes	Number of pseudo-achenes	Average percent fertile achenes/ head	Average percent pseudo-achenes/ head
1976						
Field (6-many heads/plant)	21	63.8	95	21	7.1	1.6
Rayed (one head/plant)	18	61.9	115	5	10.3	0.5
Rayless (one head/plant)	25	62.7	129	26	8.2	1.7
1977						
Field	36	46.6	257	95	15.3	5.7
Rayed	30	51.9	121	80	7.8	5.1
Rayless	60	37.7	33	102	1.5	4.5
1978						
Field	192	60.0	674	460	5.9	4.0
Rayed	191	62.1	686	365	5.8	3.1
Rayless	173	54.4	291	317	3.1	3.4
1979						
Field	164	67.6	1133	876	11.2	7.9
Rayed	155	64.7	769	309	7.7	3.1
Rayless	149	69.7	258	309	2.5	3.0

The most important points with regard to seedset are the following (Table 1). First, only a small (20.1%) reduction in seedset occurred in 1976 in which the rayed and rayless plants were mixed in the same population. Second, in 1977-1979, when the rayed and rayless populations were separated spatially, a more significant average lower percent seedset in the rayless populations prevailed (81%, 47%, 68%, respectively; mean 64%). Third, the average percent seedset per head in the field population was higher than in the rayed and rayless populations, although much more similar to the former (20% average more seedset). In 1976, however, the field population set seed at a slightly lower rate than the rayed population.

Insect visitors. —The total number of insect visitors to the rayless population is much lower (61% less) than to the rayed population on all three days monitored (Table 2). The number of different kinds of insect visitors to the rayless population also was conspicuously lower (Table 2). The only insects observed in the rayless population were Hymenoptera and the number of these was 54% lower than in the rayed population.

Discussion

Removal of ray corollas in *Helianthus grosseserratus* results in an average percent drop of 64% in seedset. Marshall and Abbott (1982) showed similar results in naturally occurring radiate and discoid individuals in *Senecio vulgaris.* They found a much lower outcrossing frequency (1%) in the rayless plants compared to rayed individuals (13-20%). Outcrossing could be measured directly in that species because ray floret production is known to be controlled by a single gene with codominant alleles. Even when pollinators were scarce or rare, ". . . the outcrossing frequency of radiate plants, though correspondingly low, greatly exceeds that exhibited by nonradiate plants" (p. 230).

A marked difference in seedset in rayed vs. rayless heads of *Helianthus grosseserratus* is dependent upon a spatial separation of plants. In 1976 when rayed and rayless plants were intermixed in the same population, only a 20.1% drop in seedset was observed, and the seedset in the field population was even lower. That the observed difference was small may relate to the fact that insect visitors, once within the food patch, use olfactory and close-range vision cues to find additional food resources, whether in rayed or rayless heads. Separating the populations by 11.5 m in 1977 and 50 m in 1978-1979 correlated with 81%, 47%, and 68% lower seedset in rayless vs. rayed populations.

Average seedset per head in the rayed population (7.9%) is not too different from the natural field condition in which plants have many rayed heads (9.9%). The observed average drop is perhaps due to the small size of the former, fewer heads per plant, and isolation (50 m) from other rayed plants, all of which would make the rayed population less visually attractive to pollinators as a food resource. It is not surprising that the percent seedset in the rayed population was closer to the field population than to the rayless population. The reasons for a low level of seedset for all populations is unknown, but it may relate to the clonal nature of this self-incompatible species whereby only pollen brought from outside the clone may lead to fertilization.

Although the reasons for the high seedset of 1977 and 1979 and low yields in 1976 and 1978 for the field populations are uncertain, they may simply reflect variations in samples that came from different numbers of clones. The seeds were collected in heads at random from hundreds of plants, and no attempt was made to take heads each year from the same individuals or from the same clones; in fact, no data exist on how many clones may have been in the field.

The drop (61%) in levels of insect visitors to the rayless vs. rayed populations in *Helianthus grosseserratus* is similar to the results obtained for *Centaurea nigra.* Lack (1982) found a 25-50% drop in visitors to mechanically created "rayless" capitula in that species (*Centaurea* is technically without ray florets, but it does have conspicuously exserted and spreading outer disc florets that appear raylike, and these are apparently what were removed). A decrease of insect visitors to rayless populations seems reasonable because these foragers, especially the Hymenoptera, are known to be attracted to visual cues

(Hassell and Southwood, 1978; Richards, 1978; Armstrong *et al.,* 1982; McCrea and Levy, 1983). The appearance of the rayless population in *H. grosseserratus* was certainly inconspicuous to the human eye. That only Hymenoptera visited the rayless population seems reasonable, because the social insects, once having located food resources, can communicate the general location of it to other individual conspecific foragers (Brittain and Newton, 1933; Heinrich, 1976, 1979; Dyer and Gould, 1983).

The preceding comments suggest strongly that the ray corollas in *Helianthus grosseserratus* are adaptive. Loss of reproductive potential in any species is likely to be disadvantageous over many generations. What is not known, however, is the effect such a reduction would actually have on population size if monitored over long periods of time. Clearly *H. grosseserratus,* because it is clonal, could survive indefinitely in this particular locality. Such continued asexual reproduction should result in few changes in the genetic structure of the populations, which in a changing environment would probably prove disadvantageous (Grant, 1981). Developmental and genetic studies should also be done to understand better the probabilities of maintenance and modification of the rayed condition during selection (*see* Stebbins, 1969, 1973, 1974, for general comments in this direction).

The main point of this paper is to demonstrate the utility of the experimental approach to assessing adaptive value of morphological structures in Compositae. Useful hypotheses can often be (and should be) generated by looking for correlations of structure and function such as was done convincingly by Grant (1950) in suggesting an adaptive role for epigyny and perigyny in the angiosperms. Predictions must be made and tests done to determine more certainly the adaptive value of reproductive and vegetative structures.

TABLE 2.—Total insects collected plus number observed (in parentheses) on 13, 15, 16 September 1979, on rayed and rayless populations of *Helianthus grosseserratus*

Insect taxa	Rayed population		Rayless population	
	Number	Percent*	Number	Percent*
Coleoptera	**6**	**3.1**		
Chrysomelidae	1	0.5		
Curculionidae	3	1.6		
Mordellidae	2	1.0		
Diptera	**17**	**8.9**		
Bombyllidae	11	5.6		
Syrphidae	3(3)	3.1		
Hymenoptera	**161**	**84.3**	**74**	**100**
Anthophoridae				
Anthophorinae	13	6.9	1	1.4
Nomadinae	4	2.1		
Xylocopinae	20(1)	11.0	13(1)	18.9
Apidae				
Apinae	96(24)	62.8	51(2)	71.6
Bombinae	1	0.5	1	1.4
Halictidae				
Halictinae	2	1.0	5	6.7
Megachilidae				
Megachilinae	1	0.5		
Lepidoptera	**1(1)**	**1.0**		
Plecoptera	**5**	**2.6**		

*The percent is of the total insects collected for each of the rayed and rayless population. Boldface numbers are summary statistics for each class of insects

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