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MINIMAL MALE/FEMALE TRADEOFFS IN ZIZANIA PALUSTRIS, A MONOECIOUS ANNUAL GRASS[1]

DORIS ARMSTRONG GOLDMAN[2]

Department of Ecology, Ethology, and Evolution, University of Illinois,
606 East Healey Street, Champaign, Illinois 61820

Because a male/female resource tradeoff is a basic assumption of many models of sex allocation in cosexual plants, statistical and manipulative methods were used to look for evidence of intersexual resource conflicts in *Zizania palustris*. In this monoecious grass, male and female investments overlap in time within each panicle and on successive panicles, and sex allocation quickly responds to environmental changes. Nevertheless, no negative correlations were found between the numbers of florets of each sex within panicles, on consecutive panicles, or on whole plants. Removing immature fruits or florets of either sex did not significantly increase subsequent investment in the other sex. The one significant tradeoff was slightly lower total fruit production on plants with exceptionally large male investment. Wild rice, therefore, fits the tradeoff assumption of sex allocation models at the population level but rarely at the individual level.

Three forms of internal competition for resources can limit reproductive output in cosexual plants: competition 1) between the vegetative and reproductive functions, 2) within each sex, and 3) between the sexes. In wild rice, *Zizania palustris* L., a monoecious annual grass, the first two forms of competition occur to a minor extent, since fruiting slightly inhibits tillering and further initiation of female florets Goldman, 1990, Chapt. 1).

In this paper, I examine *Z. palustris* for evidence of the third type of resource competition, that between allocation to male and female functions. The existence of such competition is one assumption of many models of sex allocation in plants (i.e., Charnov, Maynard-Smith, and Bull, 1976; Maynard-Smith, 1978; Charlesworth and Charlesworth, 1981; Taylor, 1981; Charnov, 1982; Ross and Gregorius, 1983). *Z. palustris* is an appropriate species to study for male/female tradeoffs because its sex allocation has low but measurable heritability (D. A. Goldman, unpublished data), and thus has not been fixed by evolution. Wild rice sex allocation is also phenotypically very plastic (Willson and Ruppel, 1984) and responds quickly to numerous changes in internal cues and the external environment (Goldman, 1990, Chapts. 1, 8, 9).

Two predictions can be made if male and

female functions compete for resources in wild rice: 1) On unmanipulated plants, the amount of investment in each sex will be inversely correlated with investment in the other sex, especially if total resources are quite limited; and 2) Experimentally preventing the use of resources by one sex will increase investment in the other sex if florets benefit directly from reduced competition with the opposite sex or indirectly from changes in hormonal gradients (cf. references in Goldman and Willson, 1986).

The first prediction is investigated in three ways, using plants grown at two densities. In wild rice, the largest temporal overlaps in male and female investment are within inflorescences (panicles) and between consecutive panicles, so regressions are used to test for negative effects of allocation to one sex on allocation to the other sex on the same panicle, and the next panicle to open, as well as on the whole plant. First, plants at the higher density are tested for negative correlations between male and female investment on consecutive panicles, since resource limitation of reproduction is marked at this density (Goldman, 1990, Chapt. 1). Second, since resource conflict between florets on two successive panicles could be diluted or concealed by the smaller effects of interactions with other panicles, sex allocation on only the first and second panicles is examined for plants at both densities. Third, since it may be that only cumulative effects are large enough to measure, differences in sex allocation are examined at the whole-plant level for plants at both densities.

The second prediction is tested by comparing sex allocation in control plants and plants that have had their male or female floral buds

Zizania palustris is an emergent annual grass of North American wetlands. Except at very high densities, each plant initiates a number of flowering stems (culms), which bloom in the order of initiation. Each new culm is shorter than the one before, has a smaller leaf area, has fewer male and female florets, and has a lower floral sex ratio (i.e., relatively fewer male florets) (Willson and Ruppel, 1984; Goldman, 1990, Chapts. 1, 8). Each culm has a terminal panicle with an apical female portion, which flowers first, and a basal male section. Plants are wind-pollinated and almost entirely out-crossed (Goldman, 1990, Chapt. 4). Fruits ripen in 1 to 3 weeks. Seed set is high, $\approx$ 80%, and varies little; seeds vary slightly in size but this does not affect their fitness (Goldman, 1990, Chapt. 2). Pollen content of male florets is almost constant (Goldman, 1990, Chapt. 3). Male florets are shed immediately after anthesis, so no resources are recovered from the empty florets, but female florets, even unpollinated ones, are not shed until fruits are ripe. Florets of both sexes are green and probably photosynthetic, but male florets appear more dependent on imported photosynthates (Goldman, 1990, Chapt. 1). A male floret on average is the genetic equivalent of 0.6 of a female floret or 0.4 of a seed (Goldman, 1990, Chapt. 7), and this varies little, since seed set and pollen production are quite uniform. Thus, the relative fitness gained by a plant through its male and female functions can be measured quite accurately by numerical counts of male and female florets. The biology of wild rice is described further in Dore (1969) and Aiken et al. (1988).

Intersexual resource conflict is possible within culms because all male investment takes place during growth of the female florets and fruits. Floret development, anthesis, and fruit development all proceed from the top of the panicle (Weir and Dale, 1960), and $\approx$ 40% of male floret growth occurs after the start of fruit growth (Goldman, 1990, Chapts. 1, 7). Fruits are ≥ 10 times heavier than male florets (Goldman and Willson, 1986; Goldman, 1990, Chapt. 7), but only 13% of fruit biomass investment comes before the end of male anthesis (Goldman, 1990, Chapt. 7).

On multistemmed plants, intersexual resource competition between culms is also possible. Consecutive culms nearly always overlap

MATERIALS AND METHODS

Regressions—Seeds were collected in Wisconsin (J. Lemberger, Wildlife Nurseries, Oshkosh, Wisconsin, personal communication) and in 1981 were planted in three pools in Champaign, Illinois, which is in the former range of *Z. palustris* (Dore, 1969). The round pools were 4 m² in area and 0.45 m deep; they were filled to 0.3 m with Drummer silty clay loam and to the top with water. Ninety-six seedlings were planted in each pool. Pools were divided into radial quarters; quarters planted with 12 plants/m² ("low density") were alternated with quarters planted with 37 plants/m² ("high density"). Plants at the edge of the pool were not discarded, giving two positions (edge vs. interior) × two densities × two replicates × three pools. Each replicate × pool will be referred to as a block.

For % seed set, 25% of panicles were bagged, including the first on each plant. Regressions were used to estimate % set on the remainder (Goldman, 1990, Chapt. 2). At senescence, total height, length, and width of the flag (= top) leaf, numbers of male and female florets, and stem order by date of anthesis were recorded for each culm. With these data, plant biomass can be determined with great accuracy ($P < 0.0001$, Goldman, 1990, Chapt. 7).

To test for inverse correlations in sex allocation on consecutive culms, partial regressions were done using the General Linear Modeling procedure with Type IV SS from the SAS package of computer programs to adjust for unbalanced data sets. Variables were orthogonally coded when appropriate, and nonsignificant terms were discarded from all regressions. 1) For 311 culms, i.e., all complete culms except the first on the 41 plants in the high density interior treatment, the number of florets of each sex was regressed against the number of florets of the opposite sex on the same stem, and florets of both sexes on the previous stem. Block, culm order, culm height, anthesis date for each sex in the panicle, and total number of culms on the plant were also included in the initial regressions. 2) For the 175 plants from all treatments for which data on the first and second stems were complete, the number of florets of each sex on the second stem was regressed against the number of florets of the opposite sex on the second stem, and the number of florets of each sex on the first stem. Block,

Source of variation	Male florets		Female florets	
	r	P	r	P
Male florets, same culm	a		0.246	0.0001
Female florets, same culm	0.520	0.0001	a	
Male florets, preceeding culm	−0.071	0.29	0.083	0.20
Female florets, preceeding culm	0.055	0.43	0.207	0.0013

a Variable not included in this regression.

density, position, culm height, data of anthesis of each sex, and total number of culms on the plant were also in the initial regression. 3) To test for cumulative tradeoffs, the total numbers of female florets and fruits were regressed against the total number of male florets on 172 plants that had no portions of panicles missing at harvest.

Floret and seed removals—Seedlings were planted at 28 plants/m² around the edges of the pools in 1982 (39 plants/pool). (The interior of each pool was also planted for another experiment; Goldman, 1990, Chapt. 6.) Plants were randomly assigned to treatments. Because some panicles were lost, the number of plants receiving each treatment varied among pools, but the treatments relevant here were replicated at least three times in each pool. 1) Twelve plants had their male floral buds removed as early as possible, while they were still under two to three layers of leaf sheath and had reached <40% of their final mass. This required unfurling of the flag leaf from around the panicle, which sometimes injured the flag leaf. 2) As controls for male floret removals, 12 plants had their flag leaves unfurled without removal of the male buds. 3) To decrease investment in fruiting, 16 plants had their female florets removed either at the start of anthesis (eight plants) or when the stigmas withered a day or two later (eight plants); fruits were ≤20% of their final mass. Plants did not respond differently to the two times of removal, and the two groups were combined after preliminary statistical analysis. 4) As controls for removal of female florets, nine plants underwent no manipulation of the female florets. All panicles were bagged and plants were measured as before. Removed florets were counted and weighed, and lengths of 78 dehusked seeds were recorded (rodents damaged the other seeds in storage). The change in biomass allocated to fruits and male and female florets with each treatment was estimated by using 2.5 mg as the final mass of a male floret, 4.8 mg as the

final mass of a female floret, and 31.2 mg as the mass of a seed (Goldman, 1990, Chapt. 7).

RESULTS

Regression analyses of individual stems—If concurrently developing male and female parts on *Z. palustris* plants compete for resources, an inverse correlation would be expected between numbers of florets of the opposite sex 1) within panicles, and 2) on consecutive panicles. The regressions did not show these relationships.

For the 41 plants growing at the interior of the high density treatment, the number of female florets on each stem was positively correlated with the number of male florets on the same stem and unrelated to the number of males on the previous stem (Table 1). Female florets were positively correlated with the number of females on the previous stem.

For the same plants, the number of male florets on a stem was not related to the number of florets of either sex on the previous stem and was positively correlated with the number of females on the same stem (Table 1). For both male and female florets, block and stem rank also were significant (Table 1).

For 175 plants from both the edge and interior of the high and low density treatments, the number of florets of each sex on the second stem was positively correlated with the number of florets of the opposite sex on the same stem, but was not correlated with the number of florets of the opposite sex on the first stem (Table 2). For both male and female florets, floret number on the second stem was positively correlated with number of florets of the same sex on the first stem. For male florets, the strongest of the three floral correlations was with female florets on the same stem. For female florets, the strongest correlation was with female florets on the first stem.

In this second set of regressions, height of the second stem on the plant, date of anthesis of the second stem, and interactions between

TABLE 2. *Correlation of the number of* Zizania palustris *florets of each sex on the second culm with florets of the opposite sex on the same culm, and both sexes on the first stem, for 175 plants grown at 0.027 to 0.082 m²/plant. For male floret regression, $r^2 = 0.630$, $P < 0.0001$; for female floret regression, $r^2 = 0.567$, $P < 0.0001$. For other factors included in regressions, see Materials and Methods*

Source of variation	Male florets		Female florets	
	r	P	r	P
Male florets, culm 2	a		0.605	0.0001
Female florets, culm 2	0.255	0.0001	a	
Male florets, culm 1	0.032	0.001	−0.100	0.32
Female florets, culm 1	−0.452	0.78	0.636	0.0001

ᵃ Variable not included in this regression.

height × density, number of stems × position in the block, and density × male florets were also significant (Table 2).

Whole-plant regressions—On 172 whole plants, total numbers of male and female florets were unrelated in linear and polynomial regressions, but there was a small but significant inverse correlation between male florets ($\delta\delta$) and the number of seeds matured:

$$\text{seeds} = 9.05 \times 10^{-2}\delta\delta - 4.55 \times 10^{-5}\delta\delta^2 + 11.60(\text{total plant mass in grams}) - 26.97$$
$$(P = 0.0001, r^2 = 0.93).$$

The extremely low impact of this tradeoff is illustrated by Fig. 1, in which the large positive effect of plant mass on the number of seeds is removed by artificially holding mass constant at 23 g, the mean for the 1981 population (Goldman, 1990, Chapt. 7). Even if all plants had the same mass, only 14% would have enough male florets to show effects of a male/female tradeoff. Seed production would increase with male floret number on most plants, reach a plateau on the 7% of plants with 900–1,000 male florets, and drop a maximum of 11% on the 7% of plants with >1,000 male florets. In reality, plant mass invariably increased as the number of male florets rose (in 1981, plants with 1,900 male florets massed 60–80 g), and the small negative effect of male floret number was offset by the large positive effect of plant mass; the largest plants not only
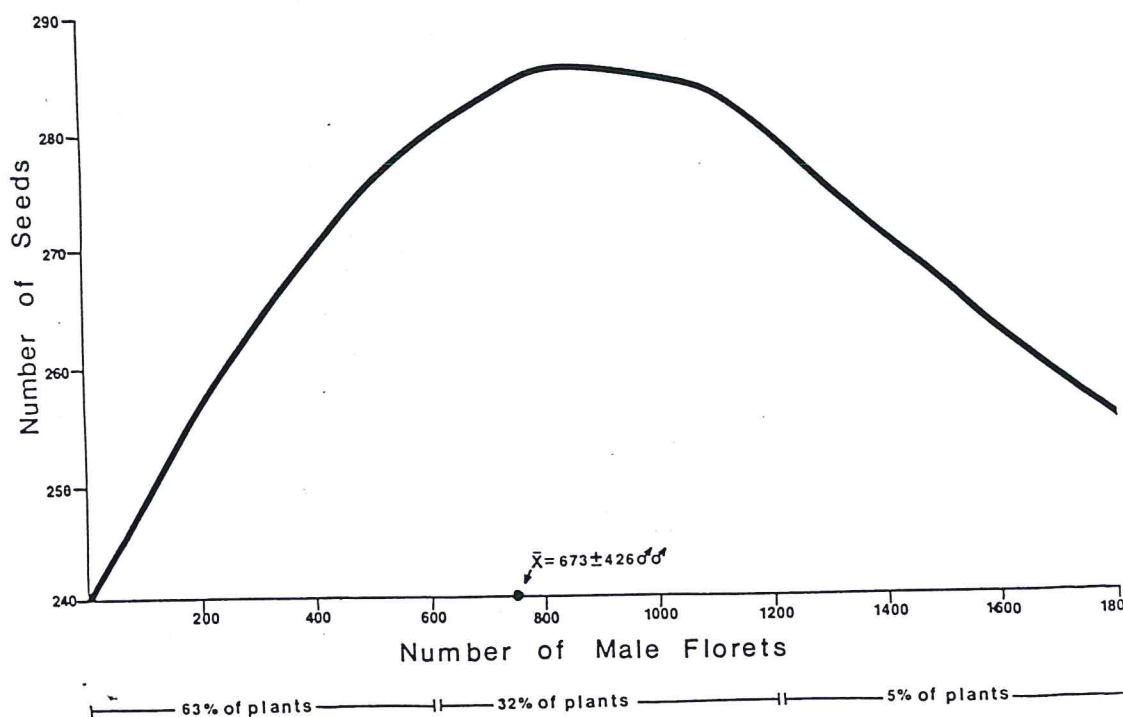

Fig. 1. Predicted relation of seed production to increasing investment in male florets. Plants from 1981, with effe of plant biomass held constant. Percent of plants in the population with a given number of male florets is marke below the graph. 673 = mean number of male florets/plant.

second culm with florets of the own at 0.027 to 0.082 m²/plant = 0.567, P < 0.0001. For other

Female florets	
r	P
0.605	0.0001
a	
-0.100	0.32
0.636	0.0001

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TABLE 3. *Shifts in estimated allocation to each sex in floret removal experiments. Mean biomass for plants in each treatment given in mg and as % change. No differences are significant*

	Control mg	Minus male florets	
		mg	% Change
Removal of male florets			
Male florets	520	260	(−100%)
Female florets	691	787	(+14%)
Female florets + fruits	3,477	4,216	(+21%)
Total reproductive allocation			
To florets	1,211	1,047	(−16%)
To florets + fruits	3,997	4,476	(+12%)

	Control mg	Minus female florets	
		mg	% Change
Removal of female florets			
Male florets	883	1,478	(+67%)
Female florets	1,104	2,150	(+95%)
Female florets + fruits	6,558	2,419	(−171%)
Total reproductive allocation			
To florets	1,987	3,628	(+82%)
... florets + ... its	7,441	3,897	(−91%)

had the most male florets, but also had the most seeds.

Floret and fruit removals—Reducing the ability of plants to invest in one sex by re- mov ng that sex did tend to enhance invest- men in the other sex, but not significantly. Plants with the pollen-producing buds re- moved did not have significantly more female florets (164 ± 29.3 vs. 144 ± 20.8 female flo- rets, $F = 0.31$, $P = 0.58$, $N = 24$ plants), nor significantly longer seeds than control plants (1.51 ± 0.037 cm vs. 1.47 ± 0.036 cm, $F = 0.69$, $P = 0.41$, $N = 78$ seeds). Manipulated plants also showed a nonsignificant ($P = 0.44$) incre ise in the number of male floral buds from 208 to 260 and an increase in the number of stems from six to nine ($P = 0.12$). Fruit set was 62% on control plants and 67% on plants with male buds removed. Changes in biomass al- location with each treatment are shown in Ta- ble 3.

Similarly, plants that had the female florets and young fruits removed to prevent full in- vestment in fruit (control plants had 76% fruit set) d d not have significantly more male florets than unmanipulated plants (591 ± 141.5 male florets vs. 353 ± 141.5 male florets, $F = 0.06$, $P = 0.81$, $N = 25$ plants). At the same time, the number of female florets initiated went from

230 to 448 ($P = 0.41$), and the number of stems went from 8 to 17 ($P = 0.81$). Absolute and % changes in biomass allocated to reproductive parts are given in Table 3. At the time of re- movals, only 10% to 20% of total dry mass investment in fruits had been made (13% of fruit biomass is husk, which is equal in mass to the female floret; Goldman, 1990, Chapts. 1, 7).

To summarize, tradeoffs between invest- ment in male and female functions of wild rice were small. Numbers of male and female flo- rets were not significantly inversely correlated on the same stem, on consecutive stems, or on the whole plant. However, in a partial regres- sion, seed production did fall slightly on plants with very many male florets, and nonsignifi- cant increases in the number of florets of each sex followed removals of immature structures of the opposite sex.

DISCUSSION

Small size of tradeoff—Only one significant male/female tradeoff was found here, and it was small. Problems with experimental design may have been partly responsible. 1) Sample size may have been too small, particularly since a significant effect was only found in uncom- monly large plants. 2) Plants were grown in rich soil, where wild rice is not nutrient-limited (Oelke and Barron, 1982; Day and Lee, 1989; Goldman, 1990, Chapt. 1). This could have prevented tradeoffs in all but the largest plants (see below). Wild rice sometimes grows in poor soils (Willson and Ruppel, 1984), where trade- offs might be more evident. 3) The impact of male removals may have been lower because male buds had already reached 40% of their final mass when removed. Total biomass of removed female parts was larger, but female florets were removed earlier, when ≈ 15% of investment in fruit had been made. Plants tended to "overcompensate" for the removal of female florets and "undercompensate" for the removal of male buds (Table 3). Also, plants with florets removed tended to have more stems than controls, so some biomass that otherwise would have gone directly into reproduction was shunted to stem initiation (Table 3). These trends suggest that resources could not readily be rechanneled to the opposite sex once de- velopment passed a certain stage. Physiological or radioactive tracer studies might reveal the movement and final location of resources di- verted from removed floral parts. 4) Biomass of florets of the opposite sex on sequential culms was not measured, but could have shown

(lower-left figure fragments) 1400   1600   1800

— 5% of plants —

orets. Plants from 1981, with effect number of male florets is marked

stronger inverse correlations than floret numbers did.

Alternatively, intersexual competition may be intrinsically low in wild rice. 1) The degree of integration of tillers is unknown, but if culms are relatively independent this might decrease competition among them. 2) Photosynthates can limit *Zizania* reproduction (Goldman, 1990, Chapt. 1), but florets and fruits do some photosynthesis (Goldman, 1990, Chapt. 7). Less than full compensation in output of reproductive biomass might be expected after removal of partially self-sufficient parts. 3) Male and female wild rice florets differ in their composition (Goldman, 1990, Chapt. 6), so competition for minerals should generally be low, the "Jack Spratt" effect of Vernet and Harper (1980), until both sexes demand large nutrient inputs. This only happened in very large plants (see below).

It might be argued that even though sex allocation in wild rice is not evolutionarily fixed and does respond to external stimuli, most results in this study were negative because wild rice sex allocation is set to the extent that it cannot be adjusted for purely internal variations in resource levels. This is not so. Wild rice plants can respond to differences in the availability of resources at even the most localized level. For example, one in 10,000 wild rice florets is perfect, and these rare florets have reduced seed size, pollen production, and % seed set (Goldman, 1990, Chapt. 12), and an inverse relation between seed length and pollen production (D. A. Goldman, unpublished data).

Proper currency for tradeoff measurements—Goldman and Willson (1986) questioned whether biomass, minerals, or other currencies are most appropriate for measuring reproductive tradeoffs. In some species biomass seems suitable (Zimmerman and Pyke, 1988; Kohn, 1989). However, in wild rice, as in some monoecious conifers (Moorby and Wareing, 1963), it appears that competition for minerals rather than photosynthates contributes more to intersexual tradeoffs.

In wild rice, mass is a good index of carbon investment (Goldman, 1990, Chapt. 6). A male floret has half the mass of a female floret and 10% of the mass of a fruit (Willson and Ruppel, 1984), and the postfruiting biomass investment ratio in wild rice is quite skewed to the female side (Willson and Ruppel, 1984; Goldman and Willson, 1986). Thus, if floret initiation is affected by intersexual competition for photosynthates, stimulation of male florets after removal of young fruits would be more likely than enhancement of female investment

after removal of male buds. Here, neither effect was significant.

Although biomass compensation was not 1 (Table 3), mineral compensation was. A single male floret contains 80% as much ash as a female floret, and 40% as much ash as a fruit (Goldman, 1990, Chapt. 6). The plateau and downturn in fruit production seen in Fig. 1 came at the points where the ash diverted to male buds equaled and exceeded the amount put into fruits.

Why are intersexual tradeoffs rarely reciprocal?—For a plant, reproduction as a female generally consumes more resources and costs more in terms of survival and further growth and fecundity (Willson, 1983). Producing a fruit generally requires more resources than fathering one, which probably explains larger investment in female organs when nutrients are more available or concentrations of growth hormones are higher (Matthews, 1963; Moorby and Wareing, 1963; Owens, 1969; Powell, 1972; Puritch, 1972; Freeman, Harper, and Charnov, 1980). It may also explain the increase in relative female investment in most flower removal experiments (Heslop-Harrison, 1957; Matthews, 1963; Moorby and Wareing, 1963; Meyer, 1966; Puritch, 1972; Freeman, Harper, and Charnov, 1980; Bawa and Webb, 1983; Silvertown, 1987). Fruits are larger and affect hormonal gradients more than male structures, so they are more vigorous nutrient sinks, and their removal typically frees more resources than removal of a male structure.

Both cosexual and dioecious plants often have male-biased investment at flowering (Goldman and Willson, 1986; Allen and Antos, 1988; Elmqvist and Gardfjell, 1988; Kohn, 1989; but see Bawa and Webb, 1983), but adding the cost of fruit production to total female effort nearly always makes it greater than male effort (Goldman and Willson, 1986; Ågren, 1988; Clark and Clark, 1988). Putting as much into male florets as into fruits is an unusually large allocation to male function for wild rice as well; mean male reproductive allocation is 50% at flowering and 20% at fruiting (Goldman, 1990, Chapt. 8).

Since individual fruits can outcompete male structures, and total investment in fruits is usually larger than male investment, female function generally has a stronger effect on male function. Reports of fruits and female flower parts inhibiting male function are much more common (Heslop-Harrison, 1957; Matthews, 1963; Moorby and Wareing, 1963; Puritch, 1972; Tormilainen, 1972; Goldman and Will-

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son, 1986; Silvertown, 1987; this study; see also Herrera, 1988) than the reverse (Hunter et al., 1969; Hadders, 1972; Goldman and Willson, 1986). In the current study, plants large enough to show male inhibition of female effort (Fig. 1) put 70% of floral biomass and 50% of final reproductive biomass (florets + fruits) into male function. Implications of this are discussed below.

Breeding system and relative size of male/female tradeoff—Avoidance of inbreeding depression is generally considered to be the major selective factor leading to the evolution of dioecy, but mechanisms that increase mating success of males and especially fruit production of females have also been proposed (Bawa, 198?; Charlesworth and Charlesworth, 1981; Charnov, 1982; Willson, 1983). An assumption of these models is that in species with some separation of the sexes, male and female functions compete for resources enough to decrease female fitness of cosexual plants (Charnov, Maynard-Smith, and Bull, 1976).

If this assumption is true, the relative cost of maleness should be higher in species or populations with greater separation of the sexes, and male/female tradeoffs should be least apparent in perfect-flowered plants and most prominent in dioecious plants. So far, this appears to be the case. For example, in hermaphroditic *Muntingia calabura*, stamen number was inversely correlated with ovary size and probability of fruit set (Bawa and Webb, 1983), but pollen production and seed or ovule number were positively correlated in *Sanguinaria canadensis* flowers (Schemske, 1978) and *Lobelia cardinalis* plants (Devlin and Stephenson, 1987). In monoecious *Cucumis sativus* (a cultivar), fruit production adversely affected male flowering but male flowers did not affect fruits (Silvertown, 1987), and here, no male/female tradeoff was evident in wild rice until massive male investment. In gynodioecious *Plantago lanceolata* and *Cucurbita foetidissima*, however, female gains nearly (Krohne, Baker, and Baker, 1980) or entirely (Kohn, 1989) compensated for the loss of male function.

More such studies are needed, especially on plants with ancestral self-incompatibility (Willson, 1983). If intersexual resource competition has contributed to the maintenance of dioecy, tradeoffs should be least common in perfect-flowered species, more common in cosexual species with some separation of the sexes, and greatest in dioecious species.

Relevance to sex allocation models—A re-

ciprocal but not necessarily linear tradeoff between allocation to male and female functions is an assumption of most models of sex allocation in cosexual plants (Charnov, Maynard-Smith, and Bull, 1976; Maynard-Smith, 1978; Charlesworth and Charlesworth, 1981; Taylor, 1981; Charnov, 1982; Ross and Gregorius, 1983; Geber and Charnov, 1986). A number of plants do show male/female tradeoffs (Bawa and Webb, 1983; Goldman and Willson, 1986; Kohn, 1989; but see Schemske, 1978; Solomon, 1985; Eriksson, 1987; Silvertown, 1987), even though investments in male and female functions may not be controlled by the same genetic and environmental factors (Stern, 1963; Tormilainen, 1972; Goldman, 1990).

A number of ecological theories depend on tradeoffs, but often the expected tradeoffs are not found in empirical studies (Pritts and Hancock, 1984; Quinn and Hodgkinson, 1984; Hughes, 1985; Galen and Weger, 1986; Giesel, 1986; Hare and Kennedy, 1986; Zangerl, 1986; Wootton, 1987). Here, the tradeoff was very small; how does this affect the application of sex allocation models to wild rice?

Wild rice is monoecious, probably due in part to selection exerted by intersexual resource competition within perfect florets, which is great enough to give a hypothetical plant with all perfect florets 15% lower male and female reproductive success at fruiting than a monoecious plant of the same size (Goldman, 1990, Chapt. 12). By comparison, in the current study the decrease in female fitness resulting from lower fruit set on monoecious plants with > 600 male florets was much smaller and was offset by a substantial increase in pollen production.

This raises the possibility that the remaining degree of resource competition between the sexes in wild rice is too small to be eliminated by selection, and the question of whether wild rice is an appropriate organism for testing models of sex allocation that rely directly on an assumption of a male/female tradeoff.

If it is important that a resource tradeoff be apparent in individuals of all sizes and conditions in species used to test these models, it may be that wild rice is more suitable for testing models that are governed directly by the relative success of the plant in passing gametes to future generations (Karlin and Lessard, 1986).

Alternatively, it may be enough that the tradeoff assumption of the allocation-mediated models is technically fulfilled by the damping of fruit production in the rare plants with very large male investment. If this is so, the small size of the tradeoff is interesting. Charnov,
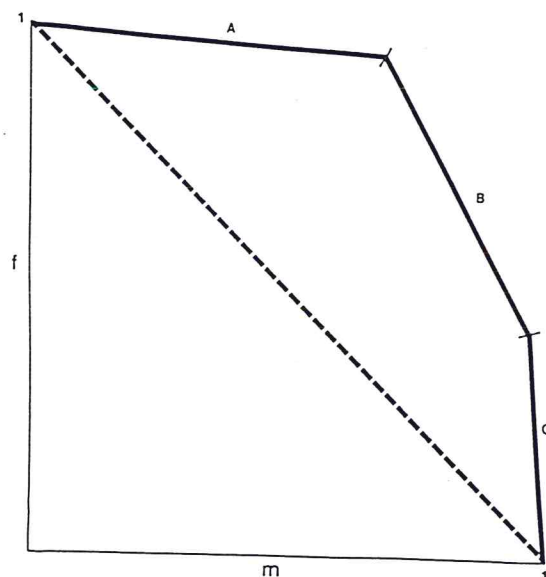
Fig. 2. Hypothetical fitness curve for monoecious wild rice plants with changing proportions of male and female florets. m = male fitness, f = female fitness, 1 = fitness of pure male or female plants. Fitness values of monoecious plants, along solid line, are greater than values for dioecious plants, along dotted line. In segment A, ♂ investment has little effect on ♀ success; in B, ♂ investment begins to decrease ♀ success, and in C, ♀ success drops quickly as ♂ investment rises.

Maynard-Smith, and Bull (1976) and Geber and Charnov (1986) discussed the case of low overlap of resource utilization between the sexes and concluded that it should allow cosexual plants to maintain unequal investment in the sexes, preventing saturation of the "fitness curve" of one sex as investment in the other increases. A similar result may apply to wild rice. The dotted line in Fig. 2 shows a linear tradeoff between male and female fitness (m and f, respectively, of Geber and Charnov, 1986); dioecy is stable below this line. The solid line shows the probable tradeoff for monoecious wild rice plants, since fruit production is almost unaffected by a unit of male investment when male allocation is low (segment A), and is most affected at high male allocation (segment C). Thus, wild rice falls in the area in which cosexuality is stable to invasion by dioecious mutants. Notably, purely female wild rice plants have been found in at least one natural population, and the trait is heritable, but gynodioecy is extremely uncommon in the species as a whole (R. E. Stucker, personal communication). For wild rice, the monoecious state prevalent in nature appears to be a stable plateau midway between a perfect-flowered state, in which male and female fitness both decrease, and a gynodioecious state, in which

the increased female fitness of pure females would not compensate for loss of male fitness in such a highly outbred plant.

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