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PATTERNS OF RESOURCE ALLOCATION IN A DIOECIOUS CAREX (CYPERACEAE)¹

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Allocation to vegetative growth and sexual reproduction was investigated throughout the growing season in the dioecious sedge, *Carex picta*, under natural conditions and following experimental manipulations. Measurements taken on unmanipulated plants showed that the sexes did not differ in the total amount of biomass they allocated to either growth or reproduction. The relatively equal investment in reproduction by the two sexes is contrary to other studies, the majority of which show greater investment in reproduction by females. Two features of the reproductive biology of *C. picta* may account for the equal investment: the fruit are relatively inexpensive because they are uniovulate and nonfleshy, and the stamens are relatively expensive because *C. picta* is wind pollinated. In contrast to the lack of differences in the amount of allocation, there were differences between the sexes in the timing of allocation to growth and reproduction: males allocated more to reproduction and less to growth up to the time of flowering, whereas females showed this pattern during the time of fruit maturation. Defoliation and inflorescence removal experiments showed that a trade-off within plants between growth and reproduction does exist. In addition, the defoliation experiment revealed a difference in the response of the two sexes: defoliated tillers on males showed a reduction in growth, whereas defoliated tillers on females did not. Overall, the data support the idea that differences in the timing of reproductive expenditure are as important as the amount of expenditure in determining many aspects of the life history strategies of the two sexes.

The principle of allocation states that because organisms are ultimately resource limited, trade-offs will exist among competing activities such as growth, maintenance, and reproduction (Gadgil and Bossert, 1970). This general principle has often been applied to investigations of resource allocation in plants, particularly when the competing activities are easily identified. For example, investigations of resource allocation in sexually dimorphic plants often show that, because females allocate more to reproduction than males, females are unable to allocate as much to other activities (Lloyd and Webb, 1977). In some species this asymmetry translates into less frequent flowering by the females as compared to males (Bawa, Keegan, and Voss, 1982; Meagher, 1984; Cipollini and Stiles, 1991), whereas in other species females show a reduction in growth (Putwain and Harper, 1972; Wallace and Rundel, 1979; Hancock and Bringham, 1980; Vitale et al., 1987; Ågren, 1988; Popp and Reinartz, 1988; Maze and Whalley, 1990). The higher cost of reproduction for females has also been suggested to divert resources in such a way that their future survival is lowered (Lloyd, 1973; Meagher and Antonovics, 1982; Oyama and Dirzo, 1988; Éscarre and Houssard, 1991). Resource allocation is also often studied in clonal species, and in addition to competition between sexual and vegetative propagation being found (Sohn and Policansky, 1977; Michaels and Bazzaz, 1986; Snow and Whigham, 1989), flowering has been shown to increase the likelihood of mortality (Law, Bradshaw, and Putwain, 1977; Michaels and Bazzaz, 1986). Moreover, Watson (1984) has shown that inflorescence production may limit ramet production by limiting the number of meristems available to become rhizomes.

However, there are examples in which trade-offs are not immediately apparent (Grant and Mitton, 1979; Conn, 1981; Sakai and Burris, 1985; Willson, 1986; Sakai and Sharik, 1988; Delph, 1990; Delph and Meagher, unpublished data). For example, differences in the timing of investment in the competing activities can influence the pattern of allocation by affecting the amount of resources acquired: females of some dimorphic species are able to invest more in photosynthetic structures such as leaves earlier in the growing season than males, because female reproductive costs are relatively low at this time (Barrett and Helenurm, 1981; Ågren, 1987; Popp and Reinartz, 1988; Delph, 1990). This pattern of allocation may allow females to acquire more resources overall, thereby enabling them to invest in fruit maturation later in the season, as well as grow the same amount as males over the whole growing season (Delph, 1990). Physiological changes associated with reproduction may also alter resource availability and reduce the amount of trade-off. In addition, it has been suggested that studies at the ramet level in clonal species with a high degree of integration between the ramets may obscure trade-offs that are occurring at the whole-plant (genet) level (Bawa, Keegan, and Voss, 1982; Pitelka, Hansen, and Ashmun, 1985). Hence, in studies concerning resource-allocation strategies, it is important to examine both the amount and timing of allocation to the various activities, and to focus at least in part at the whole plant level. Moreover, positive phenotypic correlations between growth and reproduction may obscure underlying genetic or physiological trade-offs. Hence, it has been argued that in addition to making observations on undisturbed individuals, direct experimental manipulation is a useful approach to the study of reproductive strategies (Antonovics, 1980; Partridge and Sibly, 1991).

This paper reports on an investigation of the resource allocation patterns of a wind-pollinated dioecious sedge, *Carex picta*, under natural conditions and following experimental manipulation. The following questions were addressed:

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Fig. 1. Inflorescences from a male (left) and female (right) plant of *Carex picta* at anthesis.

- 1) Are there differences between the sexual morphs in the timing and amount of allocation to vegetative growth and sexual reproduction?
- 2) Are there differences between the sexual morphs in their response to two types of experimental manipulation: defoliation of tillers and removal of inflorescences?
- 3) Do the manipulations uncover competition between growth and reproduction for resources within each of the sexual morphs?

MATERIALS AND METHODS

Study species and site—*Carex picta* is a dioecious perennial sedge that propagates through both clonal and sexual reproduction. Mature plants occur in distinct clumps that usually produce inflorescences of only one sex (see Fig. 1). Careful excavation of several clumps revealed that each clump is a clone produced by rhizomatous tillering (see also Martens, 1939). Parts of the aboveground portion of the plant persist over the winter, and we refer to these as over-wintered tillers. Only tillers that have over-wintered flower. Over-wintered tillers that produce inflorescences during the reproductive season (beginning in Feb-

ruary) are referred to as reproductive tillers, while those that fail to produce inflorescences are referred to as vegetative tillers. New tillers emerge from the basal nodes of the over-wintered tillers early in the season, and continue to grow through the time of flowering and fruiting. Late in the fall, the over-wintered tillers die and the new tillers remain until the following year (thereby becoming the over-wintered tillers for the next year).

Our study was conducted from February to September 1990 on the north shore of Griffy Reservoir, located 3 km north of the campus of Indiana University in Bloomington, Indiana. Clumps of *C. picta* were sampled from a natural population growing on a wooded south-facing slope. One hundred sixty clumps were randomly chosen from within a 15 × 40-m² area in which *C. picta* was abundant, and were randomly assigned to the various experimental treatments. Of these, 135 clones were sexed by observation of the inflorescences at the time of flowering, and the total number of tillers and the number of flowers produced on one randomly chosen inflorescence were counted for each clone.

Timing and amount of allocation in unmanipulated plants—In order to determine the timing of vegetative growth and reproduction in the two sexes, five harvests were performed at 2-wk intervals (for a 2-mo period) beginning on 6 February 1990. This time period spanned from the time before flowering up to the time when seeds were mature. Ten to 20 tillers (depending on the size of the clone) were collected randomly from each of ten clones per harvest, with any given clone being sampled for only one harvest. The tillers were separated, dried to a constant mass at 60 C, and weighed. Both vegetative tillers and reproductive tillers were collected. The reproductive tillers were broken down into their three component parts, the inflorescences (or infructescences), new tillers, and vegetative part of the over-wintered tiller, and each of these parts was weighed separately. The effects of harvest date and sex on the dry mass of new tillers were analyzed with a partially nested, mixed-model analysis of variance (ANOVA) with orthogonal contrasts. Harvest was treated as a “fixed effect,” and clone was nested within both sex and harvest date (clone[sex, harvest]) and treated as a “random effect. A similar analysis was performed with the dry mass of vegetative tillers as the dependent variable. Inflorescence dry mass was analyzed with an analysis of covariance (ANCOVA), in which the dry mass of the vegetative part of the reproductive tiller was the covariate, and sex, harvest, and clone(sex, harvest) were the main effects. Tests for significant interaction terms with the covariate were all nonsignificant, suggesting homogeneity of slopes, a necessary condition for the ANCOVA. The *F*-ratios for sex, harvest, and the sex × harvest interaction were all calculated using the clone(sex, harvest) mean square in the denominator.

An additional collection of inflorescences was taken at the time of flowering, one from each of 25 males and 29 females (haphazardly chosen), for a more detailed investigation of allocation to the parts of the inflorescence. Inflorescences from males were collected after anther emergence, but before many of the anthers had dehisced, in order to include the weight of the pollen in the measurements. This measure of inflorescence mass was more

accurate than the one calculated from the harvest during the time of flowering above (harvest #3), and therefore was used to directly compare the inflorescence mass of males and females at the time of flowering. Inflorescences were separated into the flowering portion and the peduncle, dried to a constant mass at 80 C, and the parts were weighed. A single ovule and anther was collected from an additional ten female and ten male flowers, respectively, and dried as above. Biomass of these parts was measured to within 1 μ g.

In addition to the above growth measures, a final harvest was taken in the fall at the end of the growing season (25 September 1990), in order to determine the total seasonal new tiller growth for each sex. The new tillers that had grown on each of five reproductive tillers were collected from each of 50 clones, and the new tillers were dried and weighed as above. These clones had not been sampled or manipulated (see below) previous to the final harvest. Total vegetative growth for the season (both the average mass of each new tiller and the total mass of all new tillers on a reproductive tiller) was compared between the sexes by two partially nested, two-way mixed-model ANOVAs, with sex and clone nested within sex (clone[sex]) as the main effects. Once again, sex was considered a fixed effect and clone(sex) was a random effect; the *F*-ratio for the effect of sex was calculated using the clone(sex) mean square in the denominator.

Experimental manipulations—A defoliation experiment was performed to determine whether the sexes differed in their response, and to aid in determining whether a trade-off existed between growth and reproduction. Five reproductive tillers from each of 20 clones were defoliated on 6 February by removing all of the leaves on the tiller, with the exception of the three unexpanded leaves at the growing tip. On 4 April, the five defoliated tillers and five unmanipulated tillers from the same clone were collected and dried as above. New tiller number, dry biomass per tiller, and the number of aborted inflorescences were recorded for both sexes. Inflorescences were considered to be aborted if they failed to mature their flowers. The number of seeds from each infructescence that did not abort was also recorded. Seed number was determined for one randomly chosen infructescence from each of 20 control clones for comparison.

The data on the numbers of new tillers produced were analyzed with a partially nested, three-way, mixed-model ANOVA with clone(sex) as a random effect and sex and defoliation treatment as fixed effects; because the interaction terms were not significant, they were pooled with the error term in this analysis. All effects were tested over the error mean square except the sex effect, which was tested over the clone(sex) mean square. The data on the average mass of new tillers were analyzed with the same type of ANOVA as that described for number of new tillers. The *F*-ratio for the different effects was calculated using the error mean square in the denominator except as follows: the sex effect was tested using the clone(sex) mean square, and the treatment effect was tested using the treatment \times clone(sex) interaction mean square.

An additional experiment was performed, in which inflorescences were removed at an early stage in their development, and the subsequent effect of this manipulation

TABLE 1. ANCOVA summary table for the dry mass of inflorescences for the three harvest dates up to the time of flowering. Inflorescences were in full anthesis during harvest #3. The model $R^2 = 0.84$

Source of variation	df	MS	F	P
Covariate				
Tiller mass (vegetative part)	1	242	9.2	0.004
Main effects				
Sex	1	1,802	24.3	<0.001
Harvest	2	1,445	19.5	<0.001
Sex \times Harvest	2	175	2.4	0.121
Clone(sex, harvest)	19	74	2.8	0.002
Error	55	26		

on the amount of vegetative growth was measured. Four reproductive tillers from 20 clones were randomly chosen, and the developing inflorescence was removed from each on 18 February. Inflorescences were small and enclosed by the leaves near the growing tip at this time. On 4 April the four inflorescence-removal tillers and four control tillers from the same clone (that had been matched by length and leaf number with the removal tillers prior to the treatment) were collected. Each new tiller produced on both types of tillers was separately dried and weighed, as above. Data on new tiller number and dry mass were analyzed with an ANOVA as described above for the number of new tillers in the defoliation experiment.

RESULTS

Sex ratio and size—Among the 135 clones censused at flowering, 1.5% had mixtures of male and female tillers, and 3.7% did not flower. Of the remaining 128, 75 were male and 53 were female, indicating that the population sex ratio was marginally male-biased ($\chi^2 = 3.78$, $P = 0.052$). The total tiller number per clone did not differ between males and females, averaging 50.1 ± 20.39 (SE) and 52.6 ± 20.18 , respectively ($P > 0.10$). Moreover, males and females did not differ in the percentage of tillers that produced inflorescences (26.6% on males vs. 34.9% on females; $P > 0.10$). On average, inflorescences on males exhibited more flowers than those on females, with 95 ± 5.1 and 41 ± 2.8 flowers per inflorescence, respectively (one-way ANOVA, $t = 9.22$, $P < 0.001$). Hence, the censused population contained almost 2.4 times as many male as female flowers.

Reproductive tillers—Reproductive tillers were broken down into their three component parts (inflorescence, old vegetative portion, and new tillers) and analyzed separately. There was a significant sex effect on the size of inflorescences (Table 1). Inflorescences on both sexes increased in size up to the time of flowering, with the inflorescences on the males already being larger than those on the females at the time of the first harvest and almost three times heavier at the time of the second harvest (Fig. 2). However, female inflorescences showed a large increase in size between the second and third harvest. Independent of sex, larger tillers produced larger inflorescences, as indicated by a significant covariate effect (tiller mass), and in addition, inflorescence mass differed among clones (Table 1).

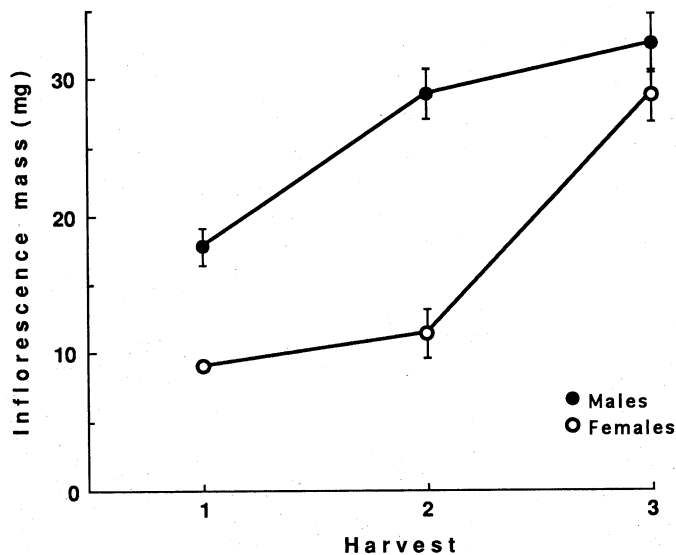


Fig. 2. A comparison of the dry biomass of inflorescences on males and females taken at three 2-wk intervals. The inflorescences were flowering at harvest #3. Values are means \pm standard errors.

Analysis of the inflorescences collected for detailed measurements at the time of flowering indicated that males invested significantly more biomass in each than did females ($36.9 \text{ mg} \pm 2.25$ vs. 31.3 ± 1.41 , respectively; one-way ANOVA, $t = 2.15$, $P = 0.036$). This greater investment per inflorescence is a consequence of males allocating significantly more to the flowers themselves (one-way ANOVA, $t = 3.17$, $P = 0.003$); the portion of the inflorescence containing the flowers weighed, on average, $25.4 \text{ mg} \pm 1.25$ on males and 20.5 ± 0.92 on females. Anthers weighed an average of $64 \mu\text{g} \pm 5.1$ per anther and $9.6 \text{ mg} \pm 0.59$ per inflorescence, comprising 38% of the biomass of the flowering portion of the male inflorescences (see Fig. 1 for a view of the anthers). Individual ovules within each female flower averaged $79 \mu\text{g} \pm 9.0$. The two sexes invested equally in the peduncles supporting the flowering portion of the inflorescence (one-way ANOVA, $t = 0.54$, $P = 0.59$).

The old vegetative portion of reproductive tillers did not grow up to the time of flowering (Table 2), and began to lose biomass subsequent to that time as leaf-tips turned brown and were shed. An ANOVA showed that the dry biomass of the old vegetative portion did not vary significantly with harvest date ($P = 0.85$), clone ($P = 0.24$), or sex ($P = 0.85$), and there was no sex \times harvest interaction ($P = 0.61$).

In contrast, the timing of the growth of the new tillers growing from the nodes of the reproductive tillers differed significantly among clones and between the two sexes (Table 3). Biomass allocated to new tillers growing on

TABLE 2. Dry mass of the vegetative portion of reproductive tillers during three successive harvests up to the time of flowering (in mg, mean \pm SE)

	Harvest		
	1	2	3
Males	338 ± 37.2	307 ± 48.2	321 ± 29.1
Females	250 ± 23.9	380 ± 24.6	316 ± 32.2

TABLE 3. ANOVA summary table and orthogonal contrasts for the dry mass of new tillers produced on reproductive tillers during five successive harvests. The model $R^2 = 0.59$

Source of variation	df	MS	F	P
Harvest	4	19,621	19.53	<0.001
Clone(sex, harvest)	33	1,005	2.04	0.001
Sex \times harvest 1	1	104	0.21	0.65
Sex \times harvest 2	1	46	0.09	0.76
Sex \times harvest 3	1	5,768	11.72	<0.001
Sex \times harvest 4	1	225	0.46	0.50
Sex \times harvest 5	1	10,193	20.72	<0.001
Error	204	492		

reproductive tillers increased significantly with harvest time on both sexes, but the pattern of growth differed (see Fig. 3A): new tillers on females were significantly larger than those on males at the time of flowering (harvest #3), whereas they were larger on males later in the season when fruit were mature (harvest #5).

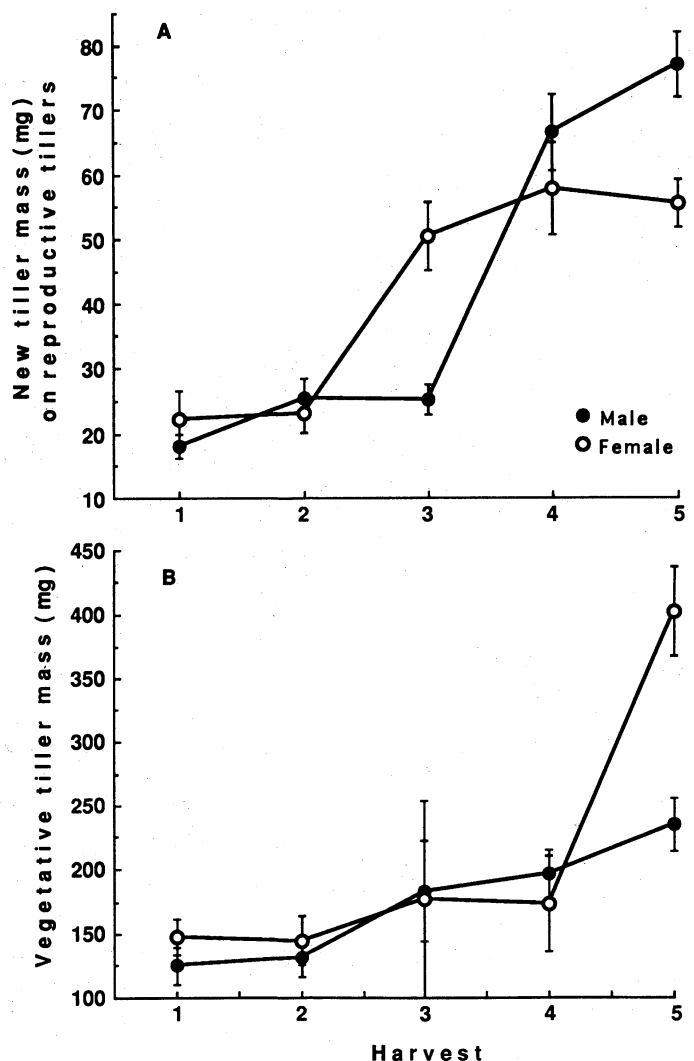


Fig. 3. A comparison of the dry biomass of tillers on males and females taken at five 2-wk intervals. Plants were flowering at harvest #3 and seeds were mature at harvest #5. A. New tillers growing on reproductive tillers. B. Vegetative tillers. Values are means \pm standard errors.

TABLE 4. ANOVA summary table and orthogonal contrasts for the dry mass of vegetative tillers during five successive harvests. The model $R^2 = 0.55$

Source of variation	df	MS	F	P
Harvest	4	158,107	19.61	<0.001
Clone(sex, harvest)	33	8,062	0.94	0.57
Sex × harvest 1	1	795	0.09	0.76
Sex × harvest 2	1	2,772	0.32	0.57
Sex × harvest 3	1	2	0.00	0.99
Sex × harvest 4	1	829	0.10	0.76
Sex × harvest 5	1	191,631	22.26	<0.001
Error	120	8,609		

Over the entire season, the sexes did not differ in the amount of dry mass allocated to either reproduction or growth of the new tillers produced on reproductive tillers. A comparison of the dry mass of male inflorescences at the time of flowering with ripe female infructescences (i.e., when each were at their heaviest weight) showed that males and females did not differ significantly in their allocation of biomass to reproduction (32.5 ± 2.16 [SE] vs. 31.5 ± 1.34 , respectively; one-way ANOVA, $t = 0.45$, $P = 0.66$). Additionally, neither the average dry mass of each of the new tillers (185 ± 18.1 for males vs. $163 \text{ mg} \pm 25.1$ for females, $P = 0.47$), nor the total new tiller dry mass per reproductive tiller (384 ± 27.5 vs. $333 \text{ mg} \pm 37.2$, $P = 0.41$) was significantly affected by the sex of the clone, although total new tiller dry mass did differ among clones ($P < 0.001$).

Vegetative tillers—Vegetative tiller growth showed a slightly different pattern of growth than did reproductive tillers (Fig. 3B). No effect of clone could be detected, but once again, growth increased through the season as evidenced by a significant harvest effect (Table 4). The two sexes differed only at the last harvest, with the vegetative shoots on females being significantly larger than those on males.

Experimental manipulations—We predicted that by defoliating reproductive tillers we would observe 1) a reduction in the amount of new growth that the tiller was capable of, in terms of new tiller number and/or biomass, and/or 2) a reduction in allocation to reproduction. Reduced allocation to reproduction could take the form of greater abortion of inflorescences on defoliated as compared to control tillers, a reduction in inflorescence size, or lastly, for the females, a reduction in seed set.

Males and females did not differ in the number of new tillers that they produced following defoliation: the number of new tillers differed significantly among clones of

TABLE 5. Results of two two-way analyses of variance on the average weight of new tillers for plants in each defoliation treatment

Source of variation	Control			Defoliated		
	df	F	P	df	F	P
Clone(sex)	18	3.59	<0.001	18	1.97	0.022
Females	9	6.00	<0.001	9	2.40	0.019
Males	9	1.18	0.317	9	1.54	0.149
Sex	1	0.29	0.600	1	6.08	0.024
Error	80			78		

TABLE 6. Average dry mass of new tillers on control and defoliated tillers of male and female plants (in mg, mean \pm SE)

Treatment	Males	Females
Control	45.7 ± 4.74	52.4 ± 6.56
Defoliated	37.1 ± 3.86	55.8 ± 4.54

both sexes ($P = 0.038$ for females and $P = 0.021$ for males), but no effect of sex could be detected ($P = 0.482$). No significant effect of defoliation treatment could be detected either ($P = 0.18$), although the trend was an increase in new tiller number on the defoliated tillers of both sexes (males: 1.20 ± 0.12 [SE] on control vs. 1.31 ± 0.11 on defoliated; females: 1.06 ± 0.12 vs. 1.22 ± 0.09).

The average weight of new tillers showed a different pattern. We did not detect a significant sex \times defoliation treatment interaction effect, but there was a significant clone(sex) \times defoliation treatment effect ($F_{18,158} = 1.82$, $P = 0.027$). We therefore separated the analyses into a partially nested, two-way, mixed-model ANOVA for each defoliation treatment, with clone(sex) and sex as main effects; the denominator mean square for the sex effect F -ratio was the clone(sex) mean square. The control tillers on males and females showed no significant differences in the average weight of new tillers, but the average weight differed significantly among female clones (Table 5). In contrast, the defoliated tillers of females were significantly heavier than those of males, and once again, there was significant variation among female clones. Hence, defoliated tillers on female plants did not show a reduction in growth, whereas those on male plants did (Table 6). Nonparametric Kruskal-Wallis tests for the effect of sex in each defoliation treatment revealed significance results that corresponded with the ANOVA results.

The frequency of abortion of inflorescences was significantly different between the sexes and treatments (Fig. 4). Overall, females showed a greater tendency to abort their inflorescences than did males ($\chi^2 = 6.94$, $P = 0.031$). Defoliated tillers on both sexes aborted their inflorescences more often than control tillers ($\chi^2 = 14.70$, $P =$

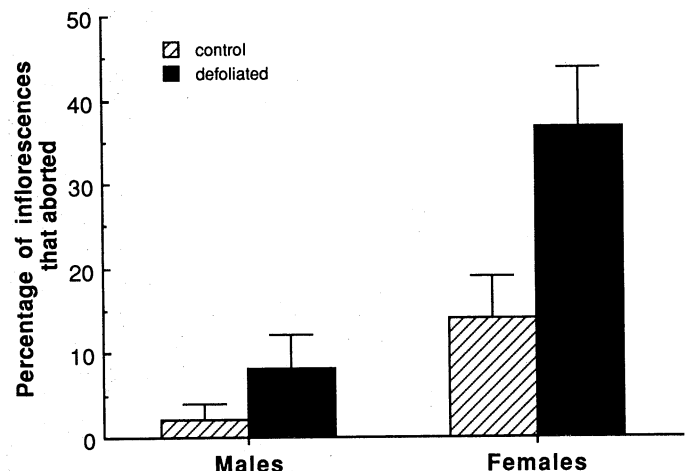


Fig. 4. The percentage of inflorescences that aborted on tillers that were defoliated early in the growing season and on unmanipulated (control) tillers, on both males and females. Values are mean \pm standard errors.

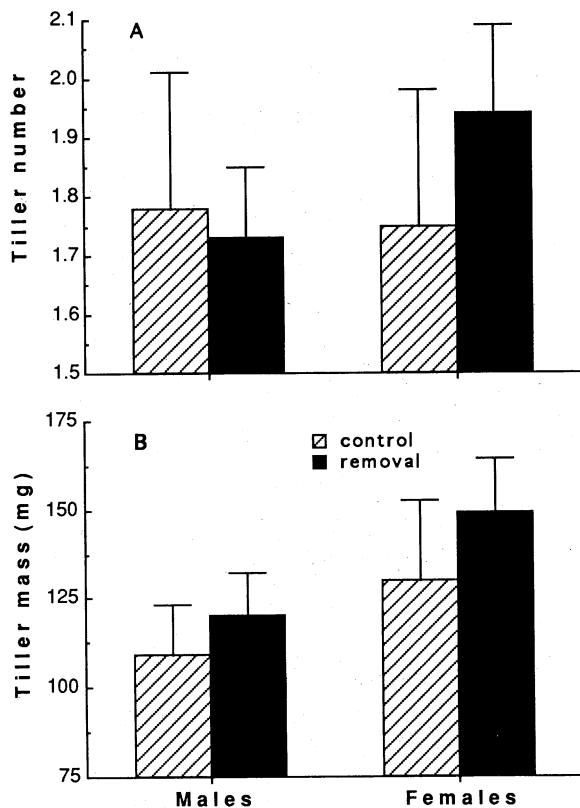


Fig. 5. The effect of removing developing inflorescences from reproductive tillers on the number and size of the remaining vegetative portions of the tillers, on both males and females. A. Number of new tillers produced. B. Dry biomass of new tillers. Values are means \pm standard errors.

0.001). Defoliated tillers on males aborted their inflorescences 4.1 times more than control tillers, whereas defoliated tillers on females aborted theirs only 2.6 times more often; however, there was no significant sex \times treatment interaction indicating that neither sex was more or less likely to abort their inflorescences in response to the defoliation. Lastly, the defoliated tillers on females that did not abort their inflorescences did not differ significantly from control plants in terms of the number of seeds they produced per infructescence (31.2 vs. 33.3, respectively; t -test, $t = 0.78$, $P = 0.44$).

We predicted that removal of developing inflorescences would cause an increase in the amount of vegetative growth within the tiller, and taken together, the results confirm this prediction. New tiller number was not significantly affected by the inflorescence removal treatment (Table 7).

TABLE 7. Results of three-way analyses of variance on the average number and dry mass of new tillers on inflorescence-removal and control tillers of males and females. The interaction terms were nonsignificant and therefore pooled with the error

Source of variation	New tiller number			New tiller dry mass	
	df	F	P	F	P
Clone(sex)	17	1.66	0.065	5.07	<0.001
Sex	1	0.66	0.428	0.55	0.468
Treatment	1	0.54	0.463	6.44	0.013
Error	95				

None of the main effects (or interactions) were significant for the number of new tillers produced, although females slightly increased their production of new tillers, while males slightly decreased theirs (Fig. 5A). In contrast, total new tiller biomass was significantly greater in inflorescence-removal tillers as compared to control tillers in both males and females. Females showed a slightly greater response than males (Fig. 5B); however, both the sex effect and sex \times treatment interaction were nonsignificant. In addition, there were significant differences among the clones (Table 7). Overall, both females and males responded by increasing the size of the new tillers, but not by altering the number of new tillers produced.

DISCUSSION

In contrast to what has been found for most of the dimorphic plant species that have been investigated, males and females of *C. picta* did not clearly differ in the proportion of their biomass allocated to reproduction. By taking into account the biomass of both the reproductive and vegetative portions of tillers, we found that both sexes allocated on average 10% of the biomass of reproductive tillers to sexual reproduction. Furthermore, we found that, of those plants that flowered, the sexes did not differ in the proportion of tillers that were reproductive.

Certain aspects of the reproductive biology of *C. picta* may account for the observed similarity between males and females in their allocation to reproduction. It is worth noting that these aspects are shared by buffalograss, *Buchloe dactyloides*, another dioecious species that also shows equal reproductive effort by the sexes (Quinn and Engel, 1986). First, the flowers of *C. picta* are uniovulate and nonfleshy. During fruit set, biomass is added only to the single ovule as it develops into an achene, resulting in relatively little biomass being added from the time of flower opening and seed ripening. This contrasts with other dioecious species that have a substantial portion of their reproductive biomass invested in the production of their fruit (see for example Lloyd and Webb, 1977; Hancock and Bringham, 1980; Ågren, 1988; Allen and Antos, 1988; Oyama and Dirzo, 1988; Korpelainen, 1992). In these species, investment may include addition to the biomass of many ovules per fruit, fruit walls, and/or the fleshy portion of the fruit.

A second feature of the reproductive biology of *C. picta* that appears to contribute to the similarity of investment in reproduction by males and females is the larger investment that the males make in inflorescences as compared to females. Thus, even though females invest resources in fruit and the males do not, the two sexes invest the same amount in reproduction overall. Unlike many previously studied species in which males allocated more to flowering than females because of a larger investment in attractive perianth parts (see Bell, 1985), *C. picta* has no perianth. Instead, we found that males invest more in flowers because of a relatively large investment in stamens: stamens comprised over one-third of the biomass of the flowering portion of the male inflorescences. This high investment in pollen is not surprising given that *C. picta* is wind pollinated. Allocation to stamens in obligately xenogamous species has been shown both theoretically (Charlesworth and Charlesworth, 1981) and em-

pirically (Cruden and Lyon, 1985) to be greater than in either facultatively xenogamous or autogamous species. Furthermore, Cruden and Lyon (1985) found that the dry mass of staminate inflorescences was greater than that of pistillate inflorescences in all four of the wind-pollinated species that they investigated. Most of the previous studies on dioecious species comparing sex expenditures have been on biotically pollinated, rather than wind-pollinated, species. Further studies may show that the generally held notion that females spend more on reproduction than males does not apply as often to wind-pollinated species.

Although the sexes of *C. picta* did not differ in the amount of allocation to growth and reproduction, they did differ in their timing of investment. Because males spent more on flowering, they appeared to be unable to expend as much energy on vegetative growth as compared to females at that time. Allocation to reproduction was reversed during the time of fruiting, with the females spending more than the males, and consequently the degree of investment in growth alternated as well. This pattern of growing less during the phase in which reproductive costs are highest has also been shown for other species. In the subdioecious shrub *Hebe subalpina*, females spend twice as much on reproduction overall as males, but because they spend less on reproduction during the flowering period they are also able to grow more early on. Consequently, females are able to acquire more resources through the growing season and therefore grow the same amount vegetatively as the males (Delph, 1990). Similarly, females of the dioecious clonal plant *Aralia nudicaulis* put more into vegetative growth than males before anthesis because investment in flowers is lower for the females (Barrett and Helenurm, 1981). Clearly, the observed resource allocation patterns of these three species are partly a consequence of an interaction between the timing of investment and the amount of investment. This type of interaction has been modeled theoretically by Burd and Head (1992); they show that a pattern of early investment in male function leads to a female-biased sex allocation in hermaphrodites and may explain why many plants show unequal allocation to the two sex functions (see Goldman and Willson, 1986 for a review). Hence, the phenology of investment is emerging as an important component of both resource and sex allocation.

We found a positive phenotypic correlation between the size of tillers and the amount of investment in reproduction, which does not indicate a trade-off between growth and reproduction. However, our experimental manipulations were designed to uncover trade-offs that might exist between these two activities, as well as to uncover differences in resource allocation strategies between the sexes that might not otherwise be apparent. Considering allocation to growth vs. reproduction first, defoliation may cause a reduction in available resources that forces a trade-off in expenditure. Similarly, the removal of inflorescences at an early stage in development may force allocation of resources (that would have otherwise gone into reproduction) to other activities (Silvertown, 1987). Evidence of trade-offs between vegetative growth and reproduction was found in both our defoliation and our inflorescence removal experiments. First, we found that tillers of both of the sexes responded to defoliation by aborting significantly more of their inflorescences than

unmanipulated tillers. Second, removing the developing inflorescence on tillers of both sexes caused them to increase their allocation to growth by increasing the size of new tillers relative to control tillers. The results of both of these experiments also suggest that clones are not totally integrated with respect to the transport of carbon between ramets, and that each reproductive tiller functions as a semiautonomous "integrated physiological unit" in the sense of Watson and Casper (1984).

Experiments of this type have provided evidence for trade-offs between growth and reproduction in other dioecious species. For example, Elmqvist and Gardfjell (1988) found that severe defoliation prior to flowering in *Silene dioica* resulted in a decrease in flower initiation in both sexes, and a decrease in seed production in females. Removal of flowers from female ramets of *Rubus chamaemorus* caused them to produce larger leaves and begin producing rhizome branchlets earlier than fruit-producing ramets (Ågren, 1988). Similarly, branches on females of *Peumus boldus* from which flower buds were removed grew, whereas branches whose flowers were left intact had no growth, showing that growth was directly related to investment in reproduction (Hoffman, 1981).

In addition to providing evidence of a trade-off among activities, our defoliation experiment demonstrated differences in resource allocation strategies among the two sexes of *C. picta* that were not apparent from the observational study. We found that males and females responded differently to defoliation performed early in the season (during the time of flower development). Tillers on *C. picta* males responded by significantly reducing their allocation to vegetative biomass relative to controls, whereas tillers on females showed no reduction. This type of response had been predicted, based on the premise that because males spend more on reproduction up to the time of flowering than do females, they should show more of a reduction in preanthesis growth if resources are made to be limited (Delph, 1990). Similarly, when males and females of *Silene dioica* were defoliated prior to flowering, males showed a larger delay in flowering and a greater tendency to die than the females (Elmqvist and Gardfjell, 1988). These sets of results complement a study on *Hebe subalpina* in which defoliation was performed after flowering, but before fruiting, which showed that females cut back significantly on growth during the time of fruiting whereas males did not (Delph, 1990). The results of all of these defoliation experiments show essentially the same pattern: the sex that normally allocates the most to reproduction during the period just after the defoliation shows the greatest decrease in allocation to vegetative growth. Hence, it appears that differences in the timing of investment in reproduction between the two sexes have contributed to the evolution of differences in their response to limiting resources.

Our study found that males spent more on flowering than females, and this is in accord with results from a large variety of dioecious species (Lloyd and Webb, 1977; Opler and Bawa, 1978; Wallace and Rundel, 1979; Hancock and Bringham, 1980; Barrett and Helenurm, 1981; Gross and Soule, 1981; Ågren, 1988; Allen and Antos, 1988; Elmqvist and Gardfjell, 1988; Oyama and Dirzo, 1988; Popp and Reinartz, 1988; Delph, 1990). This pattern of investment, in conjunction with the differential

response to defoliation that it has been shown to cause, could interact with herbivory to alter the sex ratio of populations. For example, if herbivory is occasionally severe enough to result in mortality, then the differential response of the two sexes to defoliation seen above could skew the sex ratio in opposing directions depending on the timing of the herbivory (Lloyd, Delph, and Elmqvist, unpublished data). If the majority of the herbivory occurs early in the growing season, then the population may be female-biased. In contrast, one would predict that if herbivory occurs late in the growing season, then females may suffer more mortality than the males, and the population would then become male-biased. Hence, the sex ratio of populations may be affected not only by the relative allocation of males and females to growth and maintenance, but also by the timing of this allocation.

In summary, we have shown that contrary to most dioecious species in which females spend more on reproduction than do males, females and males of the wind-pollinated species *C. picta* do not differ in their allocation to reproduction. Moreover, we have shown evidence of a trade-off among competing activities with our defoliation treatment, and that the interaction between the timing and amount of allocation to growth and reproduction influences the response of the two sexes to limiting resources. This type of interaction is likely to be an important one in determining patterns of resource allocation, sex allocation, and sex ratio and should be investigated further.

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