

ENVIRONMENTAL CONTRIBUTION TO FLORAL TRAIT VARIATION IN *CHAMAECRISTA FASCICULATA* (FABACEAE: CAESALPINOIDEAE)¹

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Although intraspecific variation in plant floral traits has been documented for a number of plant species, the causes of such variation are largely unknown. We first quantified floral trait variation in an Illinois prairie population of *Chamaecrista fasciculata* Michx. We then used a field experiment to determine the contribution of leaf herbivory to this variation and a greenhouse experiment to determine the contribution of leaf herbivory, and variable soil nutrient and water content to floral trait variation. Variation in environmental factors explained a significant portion of the naturally occurring variation in corolla width, ovule number, ovule size, and anther length. In the field, manual removal of 25% or more leaf area reduced ovule size and anther length (and by inference, pollen production), and delayed flowering. In the greenhouse, plants from which we removed 25% or more of their leaf area or which were given limited water produced fewer ovules than control plants. Addition of nutrients interacted with soil moisture to affect corolla diameter and ovule number. Despite our demonstration of significant environmental impacts on reproductive traits, these impacts were relatively much smaller than those on plant size, suggesting that floral traits are buffered against variable resource availability.

The production of seeds by plants is costly (Primack and Hall, 1990; Fox and Stevens, 1991; Pyke, 1991), requiring resource allocation to a suite of male and female characters. Great variation exists among plant species in how these resources are allocated to reproduction. For example, autogamous species often produce little or no floral nectar and only sufficient pollen to ensure fertilization, while xenogamous species produce large quantities of pollen and nectar to feed visiting pollinators (Cruden, 1977; Willson, 1983). Intraspecific variation in the amount and pattern of resource allocation to reproduction, although not as well documented as interspecific patterns, also exists. Significant intrapopulation variation has been found in pollen grain size (e.g., Bell, 1954; Willson and Burley, 1983; Ornduff, 1986; Stanton and Preston, 1986), pollen grain number (e.g., Stanton and Preston, 1986, 1988; McKone, 1989, 1990; Vear et al., 1990), ovule number (e.g., Schemske, 1978; Wyatt, 1981; Lubbers, 1986; Stanton and Preston, 1988; Fenster, 1991b), corolla size (e.g., Cruden, 1976; Galen, Zimmer, and Newport, 1987; Stanton and Preston, 1988), flower number (e.g., Primack and Antonovics, 1981; Lubbers, 1986; Jordano, 1989; Herrera, 1991), and in pattern of allocation to different floral traits (Kang and Primack, 1991).

Our understanding of the evolution of resource allocation to reproduction requires knowledge of the causes of this intraspecific variation. Evidence is accumulating that environmental conditions influence the magnitude of floral trait variation. For example, addition of nutrients can affect number of ovules (Vasek et al., 1987), flowers (Hoekstra and Mergen, 1957; Steinbrenner, Duffield, and Campbell, 1960; Bramlett and Belanger, 1976; Van Andel and Vera, 1977; Breen and Martin, 1981; Schlichting, 1986; Vasek et al., 1987), and pollen grains (McKone, 1989), as well as pollen grain size (Jones and Newell, 1948; Bell, 1959; Muller, 1979). Water stress can decrease flower production (Schlichting, 1986; Smith-Huerta and Vasek, 1987; Herrera, 1991), nectar production (Wyatt, Broyles, and Derda, 1992), and pollen viability (Schlichting, 1986), and is correlated with smaller pollen grains (Schoch-Bodmer, 1940; Bell, 1954). Finally, leaf removal can increase flower production (Schlichting and Levin, 1984) but decrease pollen production (McKone, 1989), depending on the timing of leaf removal relative to bud initiation (Sacchi et al., 1988; Hendrix and Trapp, 1989).

Because most previous studies have focused on a single floral trait, we have little information as to how the environment affects multiple floral traits simultaneously. In order to estimate the impact of the environment on plant fitness through changes in floral traits, we need to know impacts on all floral traits rather than just one, as reproductive fitness is the consequence of numerous floral traits (e.g., both the number of ovules and pollen grains produced contribute to total seeds produced). It is also important to consider the impact of the environment on entire flowers given that different flower parts all develop from the same meristematic tissue; changes in resource allocation to one flower part may affect allocation to others (Berg, 1960). Finally, seasonal variation must be taken into account, as resources available for reproduction likely change during the course of flowering (Marshall, Levin, and Fowler, 1985).

The goal of this study was to determine the degree to

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which environmental factors contribute to measured variation in selected floral traits for the prairie annual *Chamaecrista fasciculata* Michx. (Fabaceae: Caesalpinioideae). Specifically, we addressed three questions: 1) What level of intraspecific variation in reproductive characters, within and among individuals, occurs in a population of *C. fasciculata*? 2) To what degree do seasonality and natural and artificial folivory contribute to measured variation in reproductive characters in the field? 3) How do artificial folivory and nutrient and water stress interact to influence reproductive characters in the greenhouse? Reproductive traits measured were number of flowers produced, the timing of maturation of those flowers, number of pollen grains (as measured by anther size), number of ovules per flower, and ovule and corolla size.

MATERIALS AND METHODS

Plant natural history—*C. fasciculata* is native to the midwestern and eastern United States and is commonly found in old fields, disturbed prairies, and savannas (Steyermark, 1981). In eastern Missouri and western Illinois, seeds germinate from April to May, and flowers are produced in axillary racemes from June through October (Steyermark, 1981). Anthers dehisce by a terminal pore (Gleason and Cronquist, 1963), and bees (Bombidae, Apidae, and Anthophoridae) are the primary pollinators (Robertson, 1890; Thorp and Estes, 1975; Parrish and Bazzaz, 1979; Wolfe and Estes, 1992). One to seven perfect flowers are produced per raceme, and each flower lasts a single day. Although self-compatible, *C. fasciculata* is highly outcrossing (Fenster, 1991a).

Field study site and field experiment—The field study site was Fult's Prairie Nature Preserve in Monroe County, Illinois, about 0.5 km east of Fults, Illinois. Fult's Prairie is on top of a limestone bluff with a southwest- to southeast-facing slope. Associated species included *Andropogon gerardi*, *A. scoparius*, *Bouteloua curtipendula*, *Psoralea tenuifolia*, *Solidago* spp., *Liatris* spp., *Desmodium* sp., and *Petalostemon* sp.

On 4 July 1990, 150 seedlings of *Chamaecrista* were tagged, each 6–10 cm tall with three to four leaves and at least 1 m from the nearest neighboring study plant. Thirty-five plants per treatment (105 total) were assigned randomly to each of three leaf removal treatments (0%, 25%, 50%). The remaining 45 plants were assigned randomly to a 'natural herbivory' treatment in order to monitor natural damage by herbivores and to quantify natural variation in reproductive characters. Plants assigned to the 0%, 25%, and 50% leaf removal treatments were sprayed weekly with the synthetic pyrethrin insecticide Resmethrin (Miller Chemical and Fertilizer Corporation, Hanover, PA) to reduce subsequent damage by insect herbivores.

On 4–8 July, all plants were measured for initial height, leaf number, and length of all leaves. On 13 July, leaf removal treatments and insecticide spraying were initiated. Insects naturally damage leaves leaflet by leaflet. Thus, leaf removal treatments consisted of removing either one of every four leaflets on all leaves (25% treatment), or every other leaflet on alternating sides of the rachis on all leaves (50% treatment) by pinching the base

of the leaflet from the rachis. No leaflets were removed from plants in the 0% treatment. Throughout the season, leaflets were removed from new leaves as they appeared according to damage treatment level. We measured flower production, corolla width, and lower petal length, and collected buds during the period from 2 August to 6 October, censusing plants every 2–3 days. Because removal of flowers is known to increase flower production (Garrish and Lee, 1989), we quantified flower production (number of flowers open on census days) on 15 plants of each of the four treatment groups from which no flowers or buds were removed. For the remaining 20 plants of each treatment (30 plants in 'natural herbivory' group), we measured corolla width and lower petal length for all flowers open on a census day. If a flower bud was swollen and showing yellow, indicative of next day anthesis, the bud was removed and preserved in 70% ethyl alcohol for later dissection and measurement of ovule size, ovule number, and anther length. These measurements were made on flowers just prior to anthesis as we intended originally to measure pollen production directly (just before anther dehiscence), but this was not feasible.

Leaf damage was censused three times on the 45 unmanipulated plants (12 July, 2 August, 6 September); percent leaf area missing was estimated for each leaflet to the nearest one-fourth leaflet (Kelly, 1986). Total leaf area (in terms of one-fourth leaflets) was calculated by counting leaflets and multiplying by four. Entire leaves were considered eaten only when the petiole stub remained or the top one-third of the plant had been eaten. Otherwise, missing leaves and leaflets were assumed to have senesced naturally and were not included in the herbivory measurement. Final size measurements of field plants were taken on 2 and 6 October, with height, number of leaves, number of branches, and final status (dead or alive) recorded for each plant.

In order to determine whether Resmethrin affected plant growth, 40 of the 88 seedlings collected from Poag Road (see below) were randomly assigned to one of two treatment groups (control or insecticide spray) in the University of Missouri-St. Louis greenhouse. Each plant was randomly placed on a greenhouse bench with positions moved every 2 weeks. Foliage of the insecticide-treated group was sprayed once a week beginning on 14 July with Resmethrin. The control group received no spray, but both groups were watered regularly.

Greenhouse experiment—During 1–8 June 1990, 88 seedlings of *C. fasciculata* were collected from a disturbed sand prairie along Poag Road from an area 20 m × 100 m adjacent to a railroad track in Madison County, Illinois, approximately 16 km northeast of St. Louis. Seedlings were collected from Poag Road because no collecting was allowed at Fult's Prairie Nature Preserve. The seedlings collected were approximately 10 cm tall, with three to five leaves and cotyledons still present, and growing at least 1 m from the nearest collected seedling. These seedlings were planted into 11-cm clay pots filled with Jiffy soil mix (Jiffy Products, West Chicago, IL) and were grown in the greenhouse at the University of Missouri-St. Louis. On 21–23 June, the seedlings were transplanted to 15-cm clay pots with Pro-Mix (Premier Brands Inc., New Rochelle, NY), which provides sufficient nutrients for 3 weeks.

At this time, 48 of the 88 plants were randomly assigned to one of 12 treatment cells, with four plants per cell. The experimental design was a three-way factorial, with two levels each for water (control and water limited) and fertilizer (control and fertilized) and three levels for leaf removal (0%, 25%, 50%). Each plant was then randomly assigned to one of two greenhouse benches, with positions randomized every 2 weeks.

On 27 June, each plant was measured for initial height, number of leaves, and total length of leaves. Beginning on 27 June, the plants in the water-limited treatment were only watered once a week or more frequently when plants were wilted. Plants in the control water treatment were watered every other day or more often to prevent wilting. Plants in the control nutrient treatment were given no additional nutrients other than what they had received from the Pro-Mix. Plants in the fertilized treatment were given 300 ml of Peter's Professional Plant Food (W. R. Grace & Co.-Conn., Fogelsville, PA) (20%N-20%K-20%P) once a week beginning 3 July. We began the leaf removal treatments on 3 July, using the same technique and treatment levels used for field plants.

In order to minimize developmental or seasonal effects of variation in reproductive characters, all buds from greenhouse plants were collected 1 day prior to anthesis during a 1-week period after the majority of the plants had begun to flower. Most buds were collected during 9–14 August, with some collected as late as 23 August. Buds were preserved in 70% ethyl alcohol for later dissection. At the time of bud collection, corolla width and lower petal length were recorded for six to eight flowers from each plant. Final height, number of leaves, number of branches, and plant status (dead or alive) were measured during 23–31 August.

Flower bud measurements—For each plant, three to five buds were dissected in 70% alcohol under a binocular dissecting microscope. To measure ovule size, the ovary was dissected in a drop of aniline blue in lactophenol. The stain prevented desiccation of the ovules and provided a color contrast, since the ovules did not stain. The ovules were then counted, and a haphazard subsample of five was measured with an ocular micrometer.

Regression analysis was used to estimate the number of pollen grains based on anther length. To do this, we first macerated a single haphazardly selected anther of known length and width from 30 plants across treatments, 15 from field plants and 15 from greenhouse-grown plants. Each measured anther was macerated separately in a spot well in approximately 3 ml of saline solution (1% sodium chloride + 0.2% sodium azide to prevent fungal infection + 1 drop Triton X as a surfactant). Dissection tools were rinsed in a second well. Solutions from both wells were transferred by Pasteur pipette to a 150-ml beaker on a stir plate, the pipette and wells were rinsed with saline two and five times, respectively. Final beaker volume containing the macerated anther and the washings was brought to 100 ml. After stirring for 30 seconds, all pollen grains in 0.1 ml were counted under a light microscope. Three subsamples were counted for each anther. Multiplying the mean from these three counts by 1,000 yielded the total number of pollen grains present in the anther. Separate regressions were done for the 15 anthers from

greenhouse-grown plants and the 15 anthers from field plants, since they represent two distinct populations. The best least squares regression obtained in the greenhouse was:

$$\text{pollen grain number} = (0.65 \cdot (\text{anther length})^2 + 6.4)$$

($N = 15$ anthers, $r^2 = 0.53$, $P < 0.001$). The best least squares regression obtained in the field was:

$$\text{pollen grain number} = (0.69 \cdot (\text{anther length})^2 + 1.84)$$

($N = 15$ anthers, $r^2 = 0.68$, $P < 0.0001$). Anther length was then measured for all ten anthers of each bud at $\times 6.4$ power in lieu of counting pollen grains.

Statistical analysis—One-way and nested analysis of variance was used to test for differences in variables measured among plants (random effect) of the 'natural herbivory' treatment in the field study. Pearson product moment correlations were calculated between date of collection for a flower or bud (ignoring plant) and the magnitude of traits measured to determine seasonal changes in floral traits. Pearson correlations were also calculated among all measured traits (mean per plant) and plant size, as well as the total number of flowers produced and plant size. One-way ANOVA was used to test for experimental folivory effects (fixed) on the dependent variables (corolla width, anther length, ovule number, ovule size) measured in field plants. Calendar date on which a flower or bud was collected was used as a covariate in this analysis to control for changes that might be associated with development and/or photoperiod. The effects of treatments (all fixed) on dependent variables (corolla width, anther length, ovule number, ovule size) were tested with a three-way ANOVA in the greenhouse study. Tukey's tests were used to detect which levels of leaf removal had significant effects on reproductive characters in the greenhouse and in the field.

Residuals from the ANOVA were normally distributed (Kolmogorov D statistic, $P > 0.14$, SAS, 1985a). Variances were not homogeneous in all cases (F -max test, Sokal and Rohlf, 1981), and transformations did not improve homogeneity. However, deviations from homogeneity were not great, and analysis of variance is robust even with considerable heterogeneity of variances as long as sample sizes per treatment are equal or nearly so (Glass, Peckham, and Sanders, 1972).

RESULTS

Natural field variation—Unmanipulated plants in the field ('natural herbivory' treatment) varied for all floral traits measured. Individual plants varied significantly in corolla width ($\bar{X}_{\text{plant}} \pm \text{SE} = 3.17 \text{ cm} \pm 0.04$; $N = 22$) and ovule number ($\bar{X}_{\text{plant}} \pm \text{SE} = 9.6 \pm 0.2$; $N = 24$) (Table 1). Significant differences were also found among plants and among buds within plants for ovule size ($\bar{X}_{\text{plant}} \pm \text{SE} = 1.15 \text{ mm} \pm 0.01$; $N = 24$) and anther length ($\bar{X}_{\text{plant}} \pm \text{SE} = 3.74 \text{ mm} \pm 0.07$; $N = 24$) (Table 2). Total flower production ranged from 0 to 21 ($\bar{X}_{\text{plant}} \pm \text{SE} = 12.4 \pm 3.6$; $N = 15$). The magnitude of each of the measured reproductive characters varied over the course of the flowering period with plants producing smaller corollas and

TABLE 1. Analysis of variance of among plant variation in ovule number and corolla width.

Source	Ovule number					Corolla width				
	df	SS	MS	F	P	df	SS	MS	F	P
Plant	23	121.543	5.284	1.63	0.05	21	5.174	0.246	1.96	0.01
Error	104	336.199	3.233			144	18.084	0.126		
Total	127	457.742				165	23.259			

anthers and fewer but larger ovules as the season progressed (Fig. 1A–D).

All reproductive measures within individual flowers were highly correlated (Table 3). In contrast, there were no significant correlations ($P > 0.425$) between plant size and average magnitude of the floral traits, including corolla diameter. However, total number of flowers produced over the season was positively correlated ($r = 0.658$, $P = 0.0076$, $N = 15$) with plant size (number of leaves) at the initiation of flowering for 'natural herbivory' plants.

Mean damage increased over the season in 'natural herbivory' plants, from $10.9\% \pm 1.1$ (\pm SE) leaf area missing on 12 July, to $12.0\% \pm 1.2$ leaf area missing on 2 August and $32.3\% \pm 2.3$ leaf area missing on 6 September. Most damage was done by Lepidoptera larvae and grasshoppers. We correlated damage per plant and all the reproductive characters measured for those same plants. Number of flowers produced from 21 August through 6 September was negatively correlated with damage measured on 2 August ($r = -0.51$, $P = 0.05$), while ovule number of flowers produced from 21 August through 6 September was marginally negatively correlated with damage measured on 12 July ($r = -0.42$, $P = 0.07$).

Field experiment—Both plant size and the timing of flower production were affected by experimental herbivory in the field. On average, plant height in the 25% and 50% leaf removal treatments was 10% and 12% less than the 0% leaf removal group, respectively (Table 4). Thirty-one percent of those plants in the combined leaf removal treatments of 25% and 50% died during the course of the study, whereas only 15% of those plants with no leaf area removed died (chi-square: $\chi^2 = 3.01$, $df = 1$, $0.05 < P < 0.1$).

Experimental removal of 25% and 50% leaf area resulted in a significant 3% reduction in ovule size (Tables 4, 5). Anther length decreased 5% on average as a result of the 25% leaf removal treatment and 6.8% as a result of the 50% leaf removal treatment (Tables 4, 5).

There was no significant effect of experimental herbivory on total flower production ($F_{[2,43]} = 1.65$, $P > 0.2$), although means were lower for the 25% and 50% removal treatments compared to the 0% treatment (Table 5). However, experimental leaf removal and natural folivory delayed time of flowering (Fig. 2). Plants of the 25% and 50% removal treatments had a significantly lower (Kolmogorov-Smirnov goodness of fit: $P < 0.05$; Sokal and Rohlf, 1981) cumulative percent of flowers produced on 8 August compared to the 0% leaf removal treatment. Median flowering times by treatment (17, 20, 22, and 23 August for the 0%, natural, 50%, and 25% treatments, respectively) were marginally significantly different ($P = 0.072$, Kruskal Wallis adjusted $H = 6.95$; Sokal and Rohlf, 1981).

Leaf removal levels of 25% and 50% fell within the range of natural herbivory which occurred in 1990. On 6 September, 80% of 'natural herbivory' plants had 25% or more leaf damage. Thus, a large fraction of the plants experienced sufficient leaf area loss to affect reproductive traits. The greenhouse insecticide spray experiment yielded no effect of Resmethrin on plant height ($F_{[1,36]} = 0.05$, $P = 0.83$) and no effect on any of the reproductive characters measured ($F_{[1,37]} = 0.71$, $P > 0.40$).

Greenhouse experiment—Both growth and reproductive characters were significantly affected by the water and herbivory treatments in the greenhouse. Limited water plants were 24% shorter and had 33% fewer branches and 44% fewer leaves than control plants (Table 6). Fifty percent leaf area removal significantly reduced the number of branches by 27% (Table 6). The addition of nutrients had no effect on plant size, number of leaves, or number of branches (Table 6).

Limited water plants produced significantly fewer ovules (6%) (Table 6; Fig. 3A) than did control plants, while plants with 25% and 50% leaf removal produced ovules 7% smaller than plants with 0% leaf removal (Table 6; Fig. 3B). There were three sets of significant interaction

TABLE 2. Nested analysis of variance of within and among plant variation in ovule size ($r^2 = 0.85$) and anther length ($r^2 = 0.44$).^a

Source	Ovule size					Anther length				
	df	SS	MS	F	P	df	SS	MS	F	P
Model	127	8.895	0.070	22.75	0.0001	96	388.792	4.050	7.03	0.0001
Plant	23	2.584	0.112	36.5	0.0001	23	101.334	4.406	7.64	0.0001
Bud (plant)	104	6.311	0.061	19.71	0.0001	73	287.458	3.938	6.83	0.0001
Error	512	1.576	0.003			873	503.177	0.576		
Total	639	10.471				969	891.969			

^a Plant and bud (plant) sums of squares are the Type III SS of the SAS general linear models (SAS, 1985b).

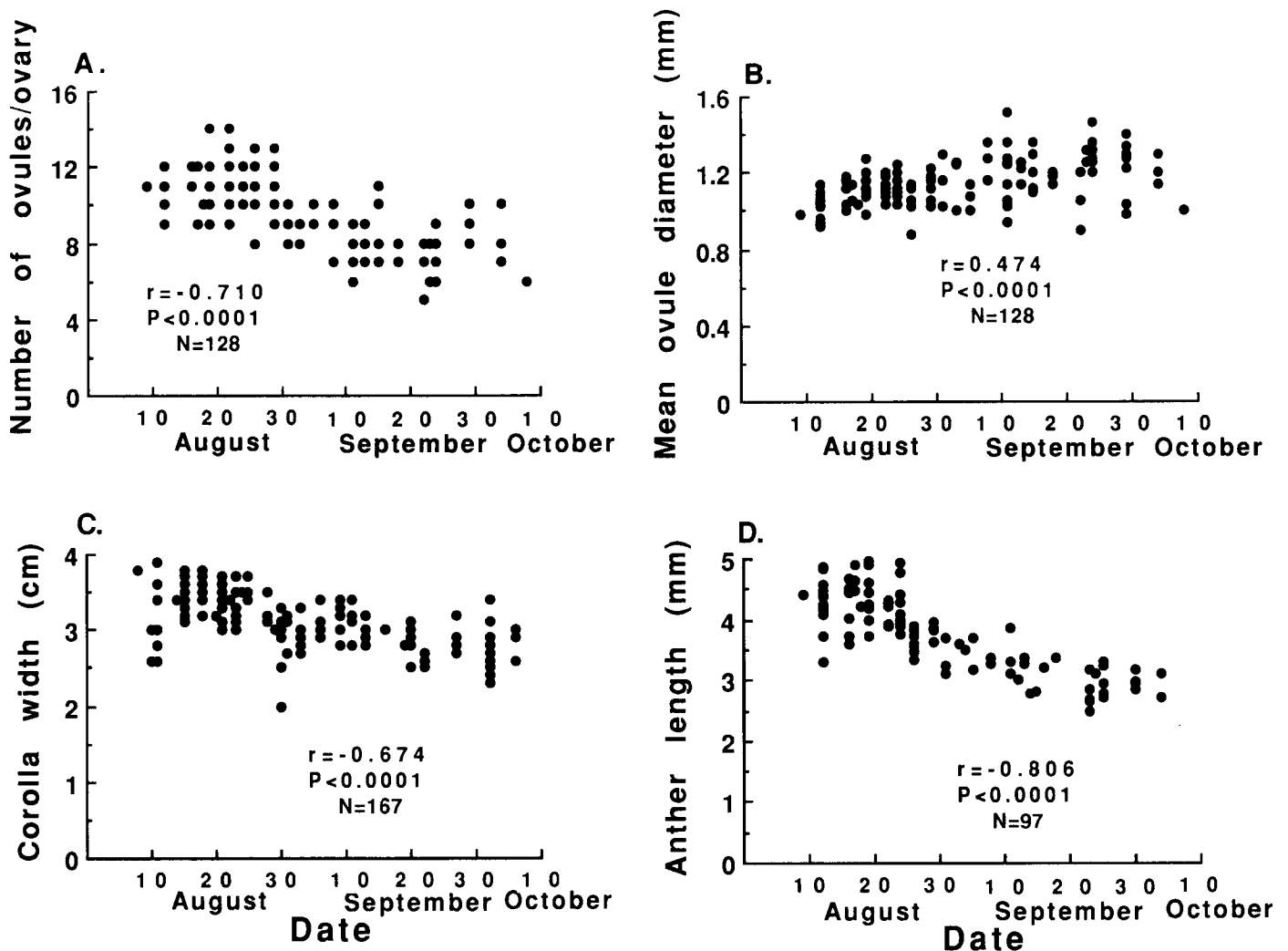


Fig. 1. Correlation of reproductive traits vs. date sampled for individual plants of *C. fasciculata* at Fult's Prairie Nature Preserve. A. Mean number of ovules per ovary, B. Mean ovule size per ovary, C. Mean corolla width, and D. Mean anther length. N = number of buds sampled; r = Pearson product moment correlation between number of days since first flower and the reproductive character measured.

terms (Table 6; Fig. 4A–C). Leaf removal decreased anther size (9%) but only when water was not limited (Fig. 4A). Limited water reduced corolla diameter (9%) but only when supplemental nutrients were not provided (Fig. 4B). Finally, addition of nutrients increased the total number of ovules produced by 4.8% when water was not limited but decreased ovule production by 7.1% when water was limited (Fig. 4C).

DISCUSSION

Individuals of *C. fasciculata* vary significantly in a number of floral traits. Variation was found among plants for all reproductive characters measured (corolla width, number of ovules, ovule size, anther length). The magnitude of these traits changed over the course of the flowering season, with smaller corollas, shorter anthers, and fewer but larger ovules produced later in the season. Late-season declines in corolla size (Stevens, Huether, and Wilson, 1972; Stace and Fripp, 1977; Kang and Primack, 1991),

ovule number (Marshall, Levin, and Fowler, 1985; Lubbers, 1986; Pellmyr, 1987; Vasek et al., 1987; Clay and Levin, 1989; Thomson, 1989; Young and Stanton, 1990), pollen grain number (Vasek et al., 1987; Young and Stanton, 1990), and in pollen grain size (Young and Stanton, 1990) have been documented in a number of other species; late-season increases in those same variables are apparently less frequent (Thomson, 1985; Thomson, McKenna, and Cruzan, 1989).

Declines in reproductive traits in the field may be due,

TABLE 3. Pearson product moment correlations among reproductive traits measured on unmanipulated plants of *C. fasciculata* at Fult's Prairie Nature Preserve ($N = 128$ flowers from 30 plants).

	Ovule diameter	Anther length
Number ovules per ovary	-0.255**	0.552***
Mean ovule diameter		-0.210*

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

TABLE 4. Analysis of variance for effect of experimental leaf removal in the field on plant traits.^a

Source	Trait							
	Final plant height				Anther length			
	df	SS	F	P	df	SS	F	P
Leaf removal	2	212.40	6.16	0.003	2	2.46	7.79	0.0006
Initial height ^b	1	505.60	29.31	0.0001	1	1.18	7.49	0.0068
Error	95	1,638.62			197	31.08		
Total	98	2,438.41			200	35.08		

Source	Trait							
	Ovule size				Percent of total flowers open by Aug. 8			
	df	SS	F	P	df	SS	F	P
Leaf removal	2	0.215	18.20	0.0001	2	1.81	9.55	0.0004
Date ^b	1	0.018	3.07	0.081	—	—	—	—
Error	253	1.494			43	4.06		
Total	256	1.730			45	5.87		

^a Treatment (leaf removal) sums of squares = Type III SS of the general linear model (SAS, 1985b)

^bInitial height and the date a flower was collected were used as covariates.

TABLE 5. Means ± SE for all reproductive characters measured on experimental plants at Fult's Prairie.^a

Treatment	N	Anther length (mm)	Number of ovules	Ovule diameter (mm)	Corolla width (cm)	Number of flowers
0% LR ^b	17	5.85 ± 0.12a	9.6 ± 0.2a	0.27 ± 0.005a	3.09 ± 0.06a	10.1 ± 1.4a
25% LR ^b	15	5.56 ± 0.20ab	9.7 ± 0.3a	0.26 ± 0.004b	3.10 ± 0.06a	8.2 ± 1.5a
50% LR ^b	13	5.45 ± 0.20bc	9.6 ± 0.3a	0.26 ± 0.006b	3.17 ± 0.06a	6.9 ± 0.8a

^a Means within a column with the same lowercase letter not significantly different (*P* > 0.05).

^b LR = leaf area removed.

TABLE 6. Three-way analysis of variance for effect of leaf removal and water and nutrient addition in the greenhouse on various plant traits.^a

Source	Final height				Final number branches				Final number leaves			
	df	SS	F	P	df	SS	F	P	df	SS	F	P
Model	12	9,477.9	3.98	0.0009	12	62.0	1.55	0.16	12	20,150.6	3.03	0.0006
LR ^b	2	73.3	0.18	0.83	2	15.7	4.56	0.06	2	1,239.5	1.12	0.34
W ^b	1	2,201.3	11.09	0.002	1	20.2	6.09	0.02	1	11,968.8	21.63	0.0001
N ^b	1	210.6	1.06	0.31	1	3.5	1.06	0.31	1	465.5	0.84	0.37
LR*W	2	417.2	1.05	0.36	2	1.3	0.19	0.83	2	1,474.7	1.33	0.28
LR*N	2	71.3	0.18	0.84	2	6.7	1.01	0.38	2	140.8	0.13	0.88
W*N	1	307.7	1.55	0.22	1	6.4	1.93	0.17	1	465.5	0.84	0.36
LR*W*N	2	130.8	0.33	0.72	2	3.2	0.48	0.62	2	928.1	0.84	0.44
HT1 ^c	1	3,308.7	16.67	0.0003	1	0.4	0.12	0.73	1	637.2	1.15	0.29
Error	32	6,350.3			32	106.4			32	17,705.3		
Total	55	15,828.2			44	168.3			44	37,855.9		

Source	Anther length				Corolla width				Total ovules				Ovule diameter			
	df	SS	F	P	df	SS	F	P	df	SS	F	P	df	SS	F	P
Model	11	2.20	1.09	0.40	11	1.69	2.08	0.05	11	29.4	1.85	0.08	11	0.0786	0.86	0.58
LR	2	0.18	0.49	0.62	2	0.18	1.20	0.31	2	5.9	2.04	0.15	2	0.0500	3.02	0.06
W	1	0.53	2.97	0.09	1	0.08	1.12	0.30	1	6.2	4.28	0.04	1	0.0004	0.05	0.83
N	1	0.02	0.09	0.81	1	0.05	0.69	0.41	1	0.3	0.24	0.62	1	0.0000	0.00	0.99
LR*W	2	1.17	3.17	0.06	2	0.36	2.45	0.09	2	3.7	1.30	0.29	2	0.0046	0.28	0.76
LR*N	2	0.07	0.17	0.82	2	0.16	1.10	0.34	1	0.5	0.17	0.84	2	0.0101	0.61	0.55
W*N	1	0.10	0.56	0.50	1	0.49	6.69	0.01	1	6.9	4.79	0.04	1	0.0036	0.44	0.51
LR*W*N	2	0.23	0.61	0.55	2	0.25	1.68	0.20	2	2.7	0.89	0.42	2	0.0099	0.60	0.56
Error	31	5.72			32	2.37			31	44.6			31	0.2569		
Total	42	7.92			43	4.05			42	74.0			42	0.3356		

^a Treatment sums of squares equal the Type III SS of the SAS general linear model (SAS, 1985b).

^b LR = leaf removal, W = water, N = nutrient.

^c Initial height (HT1) was used as a covariate.

in part, to the decreasing ability of plants to fix carbon and acquire nutrients late in the season, perhaps resulting from the cumulative effects of drought and herbivory (Marshall, Levin, and Fowler, 1985), or increased allo-

cation of limited resources to fruit development. When such decreases occur under controlled environmental conditions or when actual increases are observed, genetically controlled ontogenetic patterns may be involved (Young

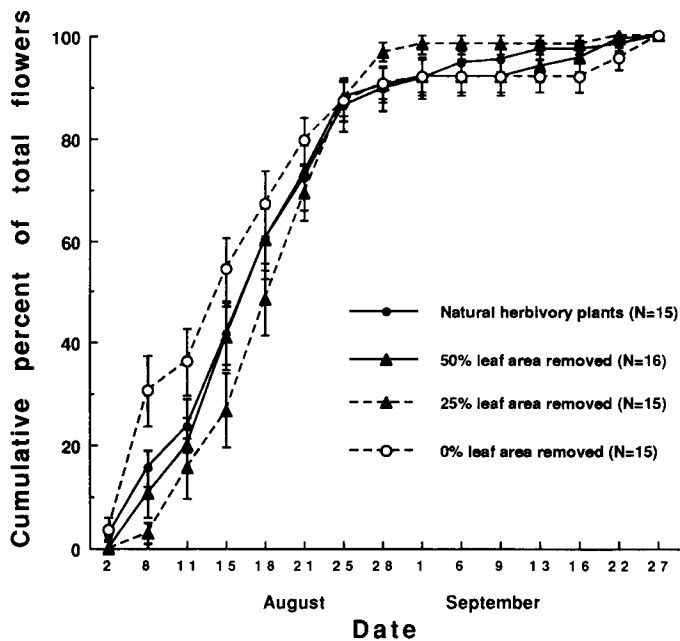


Fig. 2. Mean cumulative percentage of total flower production per plant for each census date (2 August–27 September) for three experimental folivory groups (0%, 25%, 50%) and 'natural herbivory' group observed at Fult's Prairie Nature Preserve. Error bars represent ± 1 SE. There were differences among treatments for cumulative percentage of flowers produced by the second census date, 8 August (Kolmogorov-Smirnov goodness of fit: $P < 0.05$). Median flowering times were marginally significantly different ($P = 0.072$, Kruskal-Wallis; see text).

and Stanton, 1990; Wolfe, 1992). Teasing apart the relative influence of ontogeny vs. environment is difficult when it is necessary to remove flowers in order to quantify the traits under study. Removal may affect subsequent pollen and ovule production, as resources otherwise allocated to fruit development would still be available for subsequent flower production (see Stephenson, 1981; Thomson, 1989). In our study, plants produced fewer ovules per ovary, but ovule size increased as the season progressed. Larger ovule size later in the season is associated with faster development of those ovules to mature seeds once fertilized (Lee and Bazzaz, 1982b). Flowers produced later in the season have a narrow window for seed maturation, so the production of larger ovules may provide the resources needed for such rapid maturation.

Our experimental results suggest that variation in leaf herbivory by insects and soil moisture likely contribute to the observed intraspecific variation in reproductive traits in *C. fasciculata*. The effects of nutrient addition were less pronounced (i.e., no significant main effects), although nutrient addition did modify the effect of water stress on both corolla diameter and ovule production. All traits measured were affected by our experimental treatments, in addition to being correlated sometimes with the level of natural leaf herbivory. At Fult's Prairie, *C. fasciculata* suffers varying levels of folivory and grows under varying soil moisture conditions, from exposed prairie to the edge of mesic forest. Soil nutrient availability is likely to vary as well. We assume that our experiments affected resources available to the plant, since plant size

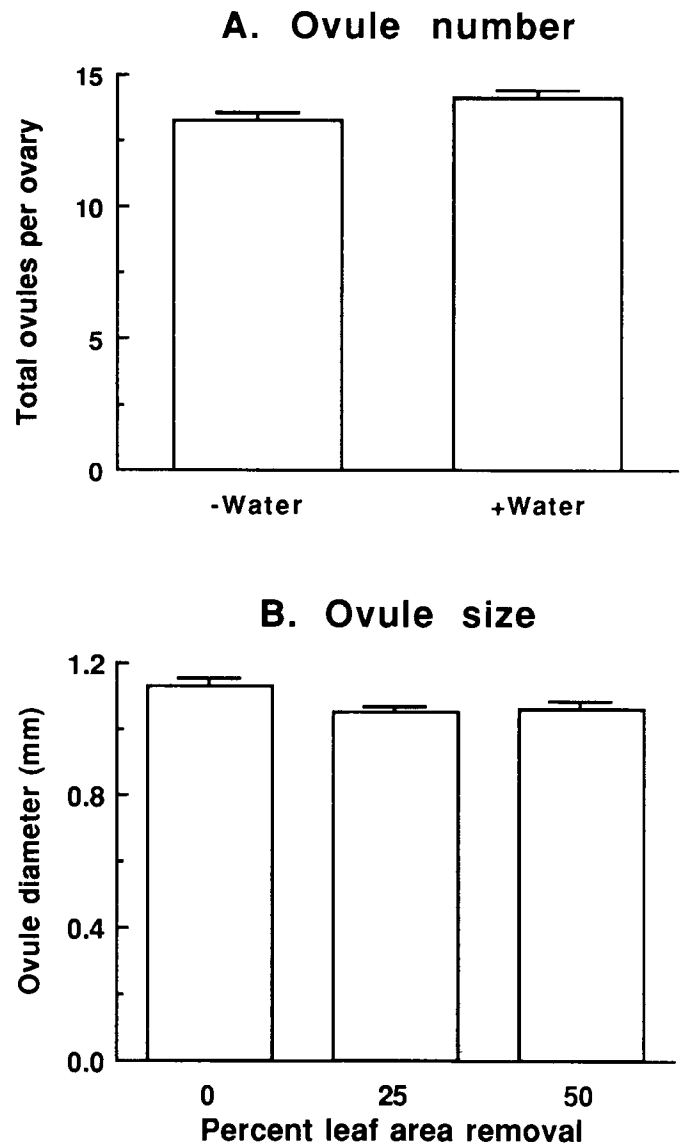
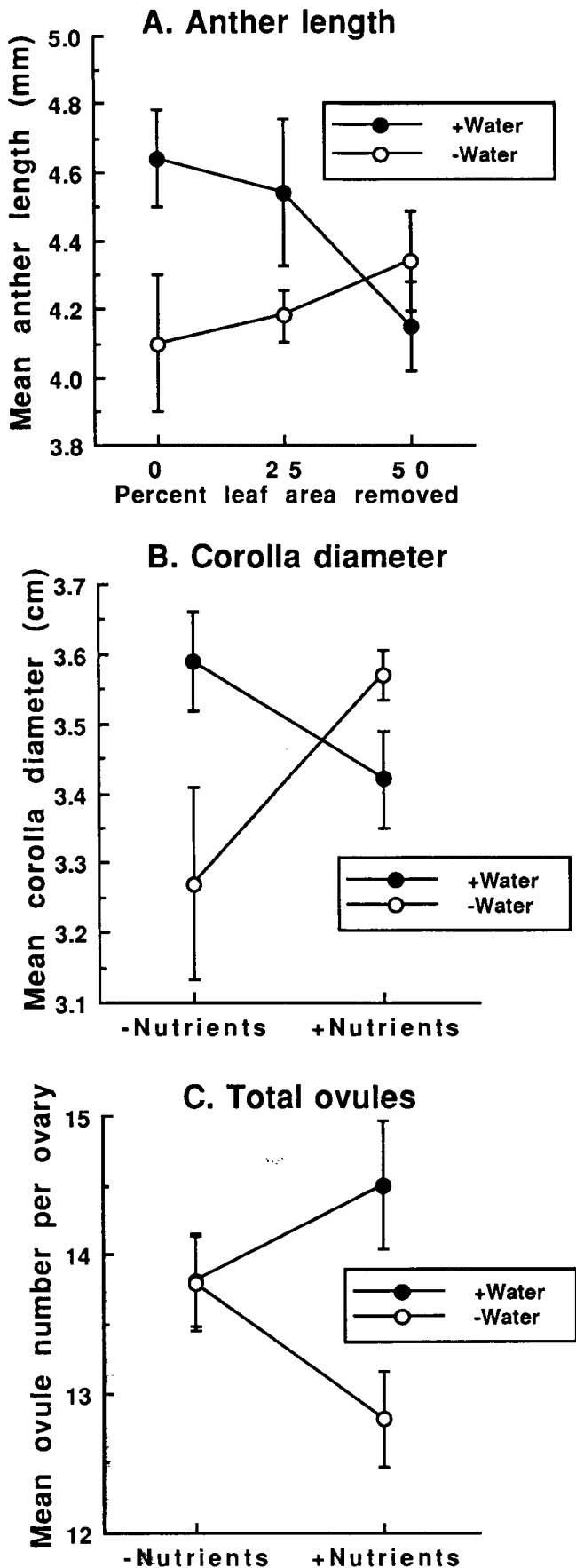


Fig. 3. Main effects of greenhouse treatments on reproductive traits of *C. fasciculata*. Error bars represent ± 1 SE. A. Effect of limited (–) and unlimited (+) water on mean number of ovules per flower (ANOVA, $F_{(1,32)} = 4.28$, $P < 0.04$); B. Effect of leaf removal on mean ovule size (ANOVA, $F_{(1,32)} = 3.02$, $P = 0.061$). Error bars represent ± 1 SE.

(plant height and number of branches and leaves) was also affected by experimental leaf damage and water stress.

To be of selective importance, the effect of water and folivory on reproductive characters must have fitness consequences. However, the relationship between variation in reproductive traits and fitness is not known specifically for *C. fasciculata*. Male fitness could be influenced by both pollen grain number and size (Stanton and Preston, 1986). Given ample pollinators and pollen recipients, individuals producing more pollen grains will father more seeds than individuals producing fewer grains. In *C. fasciculata*, the observed 5% decrease in anther size due to removal of leaf area in the field would result in approximately 10,000 (Fult's Prairie plants) or 13,000 (Poag Road plants) fewer pollen grains produced per flower.



Pollen also serves as the sole reward for pollinators in *C. fasciculata*, since the plant produces no floral nectar (Wolfe and Estes, 1992). Providing quantities of pollen as a reward to pollinators in addition to pollination obscures the relationship between pollen production and male fitness in this plant species. We did not measure pollen size and viability, but these traits also might be affected by the treatments (Schoch-Bodmer, 1940; Stanley and Linskens, 1974; Willson and Burley, 1983; Stanton and Preston, 1986).

Clearly, reduced flower production by more heavily damaged plants of *C. fasciculata* reduces the potential for seed production by the maternal plant (e.g., Wyatt, 1980; Andersson, 1988; Thompson and Pellmyr, 1989; Herrera, 1991; Devlin, Clegg, and Ellstrand, 1992), the potential for siring of seeds as a paternal plant (Fenster, 1991a), and possibly, the attractiveness of a plant as a pollen donor (e.g., Charnov, 1982; Lloyd, 1984; Rodríguez-Robles, Meléndez, and Ackerman, 1992). Larger plants of *C. fasciculata* with more flowers produce more fruit than smaller plants with fewer flowers (Kelly, 1992), but the independent effect of flower number on probability of fruit set is not known. In our study, herbivores also directly reduced the number of viable flowers produced: 28% of buds examined from unmanipulated plants were infested by larvae of an unknown species of Lepidoptera.

The observed delay in flowering time (see also Kinsman and Platt, 1984; Marquis, 1988) might decrease fitness if flowers produced later had less chance of dispersing their pollen and/or receiving pollen from other plants or had less time for maturation of fertilized ovules. A positive correlation between early flower production and seed production has been found in a central Illinois population of *C. fasciculata* (Kelly, 1992). A delay in flowering time might also change the mating structure of the population, with fewer individuals available for mating both early and late in the season (Lee and Bazzaz, 1982a; Fenster, 1991a).

An increase in ovule number (see greenhouse experiment results) could result in higher seed production, depending on the interaction between resources available for seed production, abortion rate, and subsequent attraction of pre-dispersal seed predators. Seed production in *C. fasciculata* is thought to be limited by both resources (and not pollen) and pre-dispersal seed predators (Lee and Bazzaz, 1982a). The relationship is likely to vary across sites and years, as both water availability (Kelly, 1992) and predation (Lee and Bazzaz, 1982a; Kelly, 1992) vary spatially and temporally for this plant species. There is no evidence that greater ovule number in *C. fasciculata* may enhance female fitness by allowing more opportunity for selective abortion of genetically inferior seeds (Fenster, 1991b; Sork and Schemske, 1992).

Fig. 4. Interactive effects of leaf area removal and nutrient addition with water addition on reproductive traits of greenhouse-grown *C. fasciculata*. Error bars represent ± 1 SE. A. Interaction of leaf area removal with water on mean anther length per flower (ANOVA, $F_{(2,32)} = 3.17$, $P = 0.063$). B. Interaction of nutrients with water on mean corolla diameter (ANOVA, $F_{(1,32)} = 6.69$, $P < 0.01$). C. Interaction of nutrients with water on mean number of ovules per flower (ANOVA, $F_{(1,32)} = 4.79$, $P = 0.04$).

Despite the fact that environmental factors explained a portion of the variation present in reproductive traits in *C. fasciculata*, we were able to change plant size to a greater degree than we could change reproductive traits. In addition, magnitudes of floral traits were not correlated with plant size in unmanipulated plants. In contrast, flower number was correlated positively with plant size. Because of this relative immunity of floral traits to the influence of the environment (suggesting relatively strong genetic control), it would seem that environmental impacts on plant fitness will be greater through changes in plant size (and therefore, flower and fruit number) compared to changes in characteristics of the individual flowers contributing to fitness (see also Schwaegerle and Levin, 1990). Further experimentation is needed to define the contribution of variation in reproductive traits to plant fitness.

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