Population Structure, Biomass Allocation, and Phenotypic Plasticity in Murdannia keisak (Commelinaceae)

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POPULATION STRUCTURE, BIOMASS ALLOCATION, AND PHENOTYPIC PLASTICITY IN MURDANNIA KEISAK (COMMELINACEAE)[1]

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Field and glasshouse studies were used to explain differences in plant biomass, shoot length, and reproductive effort in four populations of a wetland annual herb, *Murdannia keisak*. Populations were chosen from continually thermally disturbed, intermittently thermally disturbed, revegetating, and undisturbed portions of a floodplain forest in South Carolina, USA. Plants in the two thermally disturbed areas were shorter, flowered earlier in the autumn, and produced more and smaller seeds than plants in revegetating and undisturbed sites. Reproductive effort was higher in populations from undisturbed and revegetating sites than in the two thermally disturbed sites. Generally, differences observed in the field were not expressed in the glasshouse plants. Glasshouse experiments suggested that most of the observed among-population differences in size and reproductive effort in the field study were a result of a plastic response to water depth and light. The combination of field and glasshouse data showed that this wetland weed adjusts readily to newly disturbed habitats, thus spreading rapidly and maintaining local dominance.

In response to changing or new environments, individual plants can exhibit considerable phenotypic plasticity, or character variation (Bradshaw, 1965; Schlichting, 1986). This phenotypic plasticity may itself be under genetic control and may evolve under selection (Bradshaw, 1965; Schlichting, 1986; Sultan, 1987). At the population level, selection by the environment can also result in genetically fixed differences in certain traits (Clausen, Keck, and Hiesey, 1940; Gregor, 1946; Harper and Ogden, 1970; Jefferies, Davy, and Rudmik, 1981; Higgins and Mack, 1987; Scheiner and Teeri, 1987). Plasticity of plant traits may allow species to adjust to new environments resulting from dispersal of individuals, disturbance (Solbrig and Simpson, 1974; Pianka, 1988), or successional changes (e.g., Werner and Platt, 1976; Roos and Quinn, 1977). Fitness, furthermore, could be maintained by phenotypic variability in response to a changing environment (Pianka, 1988).

Differences in traits expressed by plants in the field can add considerably to our understanding of plant responses to specific environmental factors when they are compared with controlled laboratory or glasshouse studies (Thompson and Stewart, 1981). This comparative approach was taken to examine differences among populations of an annual wetland herb (*Murdannia keisak* (Hassk.) Hand.-Mazz.: Commelinaceae) occurring on the Savannah River floodplain in South Carolina, USA.

In this study, the population structure, biomass allocation, and character variation of *M. keisak* are described for four contrasting environments in which this species is common: two thermally disturbed sites, a shrub-dominated postthermal site, and an undisturbed site. These field populations provide the basis for an experimental approach to determine if differences among these field populations are genetically fixed or occur in response to environmental differences.

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STUDY SITE AND SPECIES DESCRIPTIONS

Field and glasshouse studies were conducted at the Savannah River Site (SRS) bordering the Savannah River in South Carolina (33°7′N, 81°40′W). The 3,020-hectare forested wetland on the floodplain is dominated by *Taxodium distichum* (bald cypress) and *Nyssa aquatica* (water tupelo) in the overstory and by herbs in canopy openings (nomenclature follows Godfrey and Wooten,1979). Several tributary streams of the Savannah River that originate on the SRS carry thermal effluent from nuclear reactors and empty into the floodplain forest. Large areas of the floodplain forest have been destroyed by this thermal pollution and replaced by populations of herbs capable of withstanding the extreme (35–40 C) thermal environment.

Four study sites were chosen in this forested wetland representing several levels of disturbance. Two sites were chosen near the mouth of Pen Branch (PB), a stream which, at the time of the study, had been carrying thermal effluent since 1954. One of these sites (CT = continuously thermal) had continually received thermal effluent, while the other (IT = intermittently thermal) had been affected intermittently (every 3–4 years). The tree canopy at both Pen Branch sites had largely been destroyed by the thermal pollution and replaced by herbs (e.g., *Leersia oryzoides, Ludwigia leptocarpa, L. decurrens, Polygonum* spp., *Typha latifolia*). A third study site (FT = formerly thermal), located in the floodplain at the mouth of Steel Creek, received thermal effluent continually from 1954 to 1968. This site was revegetating and characterized by a mosaic of successional shrubs (e.g., *Salix* spp., *Cephalanthus occidentalis, Fraxinus caroliniana*), wetland herbs, and open water (Dunn and Sharitz, 1987). A fourth, undisturbed, site (NT = nonthermal) was located on the river floodplain near Steel Creek. Water temperatures at both SC sites were near ambient Savannah River temperatures (ca. 21 C).

The physical environments differed between the PB and SC sites. At PB, water depth was about 20 cm during the growing season, while at SC it was about 40 cm. The revegetating Steel Creek site (FT) occurred beneath a canopy of willow (*Salix* spp.), whereas the undisturbed site (NT) was shaded by a canopy of *T. distichum* and *N. aquatica.* Thus the herb layer at these two sites received only about 5% of the light (ca. 75 μmol m^{-2} s^{-1}) received by the herb layer at the two Pen Branch sites (ca. 1,635 μmol m^{-2} s^{-1}).

Murdannia keisak (Hassk.) Hand.-Mazz. (Commelinaceae; syn. *Aneilema keisak* Hassk.) occurs in dense stands in thermally disturbed and in undisturbed portions of the floodplain. This species is an Asian wetland annual herb that has been naturalized in the southeastern United States (Shinners, 1962) since at least 1931 (Hotchkiss, 1940) and was probably introduced with rice seed near the end of the seventeenth century (Dunn and Sharitz, 1990a). The stem of *M. keisak* is succulent and initially upright, but by the middle of the growing season, plants branch at the nodes and lie horizontally. Adventitious roots can also form at more distal nodes so that branches and shoot tips can become rooted. In addition, the bases of stems can die, with plants remaining anchored by prolific adventitious roots formed at the lower nodes. Flowers arise (usually singly) from nodes in September or October. Flowers have two to three locules, each locule containing one to several seeds (Fernald, 1970). Little is known about the breeding system of species in this genus (Faden, 1975; D. H. Les, personal communication), although they probably are autogamous, as is common among annual hydrophilous angiosperms (Les, 1988).

MATERIALS AND METHODS

Field plants*—Murdannia keisak* plants were sampled from all four sites at monthly intervals (May to October) in 1986. All plants were counted and harvested from two 0.25-m × 0.25-m quadrats randomly located in each of the four populations. Quadrat size was limited by high plant densities. Shoot length and the numbers of nodes, branches, live leaves, and flowers, capsules, or seeds were recorded for each plant. After being washed in deionized water, plants were sorted into stems and branches, leaves, roots (primary and adventitious), and (in September and October only) reproductive structures. All harvested material was dried (60 C for 72 hr) and weighed by class of the plant material. Entire samples were ground and subsamples analyzed for mineral concentrations using the CHN Analyzer at the University of Georgia's Plasma Emission Spectrometer Laboratory.

Analysis of field data—Differences in morphological traits were assessed with one-way ANOVA (procedure in SAS, 1982). Unbiased Gini coefficients (*G*, with bootstrapped 95% confidence intervals) were used as a measure of plant biomass asymmetry, or size hierarchy (Weiner and Solbrig, 1984; Weiner, 1985). Gini coefficients were determined using a PASCAL program (Dixon et al., 1987). The Gini coefficient (G) was used to describe the degree to which biomass was concentrated among individuals in each population (Weiner and Thomas, 1986). The coefficient can range from 0 when all individuals are equal in biomass (no hierarchy or inequality) to 1 in an infinitely large population in which all individuals but one have a value of 0 (maximum hierarchy or inequality; Weiner and Solbrig, 1984).

Although reproductive effort (RE) is defined as the ratio of reproductive allocation to total plant allocation, allocation itself is often not clearly defined (Reekie and Bazzaz, 1987a). To compare differences in RE resulting from different definitions of allocation, reproductive effort per plant was determined in the following ways:

RE_1 = flower biomass/aboveground plant biomass
RE_2 = flower biomass/total plant biomass
RE_3 = flower carbon/aboveground plant carbon
RE_4 = flower carbon/total plant carbon
RE_5 = flower nitrogen/aboveground plant nitrogen
RE_6 = flower nitrogen/total plant nitrogen.

As used here, flowers included all floral organs and developing seeds. The carbon measures of reproductive effort (RE_3 and RE_4) did not include respiratory carbon and thus did not conform precisely to the definitions of Reekie and Bazzaz (1987a). Because plants at both PB sites flowered in September and October, RE estimates were calculated separately for each month. Plants at both SC sites flowered only in October. Two comparisons of RE were made among the populations. First, October RE at the PB sites was compared with October RE at the SC sites. Second, RE at the PB sites for September and October were averaged and compared to the October data from SC. Thompson and Stewart (1981) suggest summing sequential estimates of RE, although they acknowledge that this could overestimate RE. Over the course of the flowering period, it seemed more appropriate to average the two monthly RE estimates. For instance, if RE was estimated to be 0.2 and 0.4 for two successive months, the RE for the flowering period would be closer to 0.3 than to 0.6

The individual measures of RE were also compared with each other to see if population REs were ranked (Spearman rank correlation) in the same order regardless of measure used. Significantly different rankings (Kendall's coefficient of concordance) would suggest that each RE measure describes a different allocation pattern.

Glasshouse plants—Bulk seeds were collected from the extremes of the disturbance gradient (CT, $N = 221$ seeds; NT, $N = 136$) and were grown under controlled glasshouse conditions to determine if differences in plant form, biomass allocation, and RE were genetically based. Seeds were collected in November 1986 and kept moist in dark cold-stratification (5 C) for 3 months. All seeds but one germinated within 2 weeks after exposure to ca. 25 C and light. These seedlings were used in two major glasshouse experiments initiated in March 1987.

Temperature and light treatments—In the first experiment, 88 seedlings from each population were randomly selected and planted, one per pot, in 10-cm × 10-cm pots filled with commercial glasshouse potting soil. Pots were placed in one of two 1.80-m^3 steel tanks (2.95 m^2 surface area) in which four treatments were established. One tank was filled with unheated water (24 C) and the other with heated water (35 C) to simulate thermal conditions near PB. A submersible pump in each tank kept the water mixed, eliminating hot or cold spots. Pots were elevated to minimize shading by the sides of the tanks, and the water level was maintained 2 cm below the top of the soil surface keeping the soil continuously saturated. Half of each tank was shaded (top and sides) to allow only 5% of the sunlight to penetrate. This percentage represented the minimum available light in the field at Steel Creek. The experiment consisted of 22 individuals per population in each combination of water temperature and light. To minimize any effect of location in the tanks, plants within treatments were randomly moved three times during the experiment.

Plants were harvested at flowering in late October. Shoot length, masses of stems, leaves, and flowers, and numbers of branches and flowers were recorded. Root biomass, seed output, and seed size could not be determined accurately for the glasshouse plants because these plants became more entangled than did plants in the field. Flowers or capsules per plant, however, were counted and used to estimate seed output (number of flowers × three seeds per fruit determined from field plants = seed output).

Water depth gradient—Because PB plants (CT and IT) grew in shallower water and tended to be shorter than SC plants (FT and NT), a

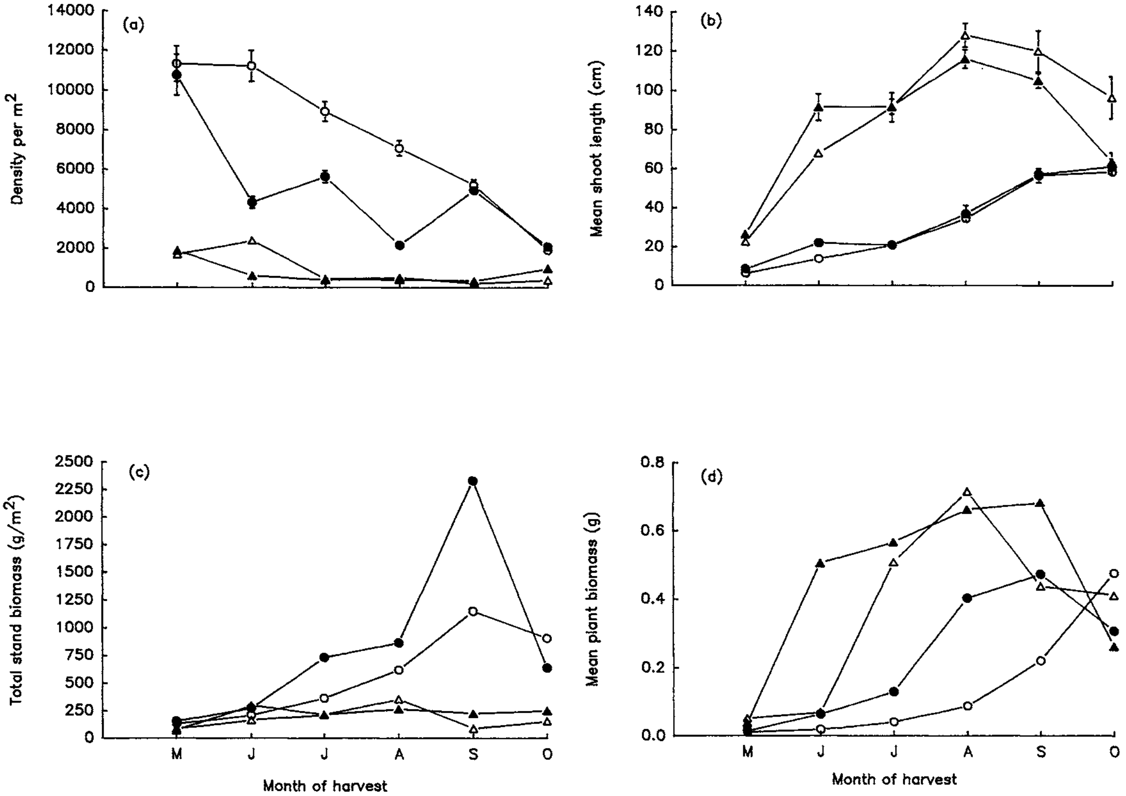

Fig. 1. Patterns of (a) mean plant density, (b) mean shoot length, (c) total stand biomass, and (d) mean plant biomass over time for four populations of *Murdannia keisak*: CT (●), IT (○), FT (△), and NT (▲). Site abbreviations are explained in text. Error bars are ± 1 SE.

second experiment was initiated to determine if water depth affected height and branching of PB plants. Pots containing CT seedlings were placed at three depths in a third tank with ambient water temperature and full sun: 1) deep flooded with shoots fully submerged; 2) flooded with emergent shoot tips; and 3) saturated soil with shoots fully exposed above the water surface ($N = 25$ plants per depth). Plants were harvested at the same time as those in the other glasshouse experiment and the same data were recorded.

Analysis of glasshouse data—A three-way ANOVA was used to assess the relative contributions of phenotypic plasticity and of genetic differentiation to variation in morphological and reproductive traits of *M. keisak.* Treatments were population (seed source), temperature, and light. Plasticity of a plant character is indicated by significant effects of temperature or light. A significant population term would suggest some genetic difference between populations (Schlichting and Levin, 1984), although some maternal effect cannot be ruled out (Primack and Kang, 1989). Interaction terms were included in the statistical analysis, but none were found to be significant and thus they are not reported here. Because roots protruded from pots and became entangled and because carbon and nitrogen were not determined, reproductive effort (RE) of plants grown in the glasshouse was measured only by RE$_1$.

RESULTS

Field plants—*Plant density and growth*—Densities of *M. keisak* were significantly higher at the two PB sites than at the two SC sites throughout much of the growing season (Fig. 1a). Densities at PB declined throughout the season; at SC, densities declined early in the growing season, then stabilized at <300 individuals per m^2.

With the exception of October, mean shoot length of SC plants was significantly greater than that of PB plants throughout the growing season (Fig. 1b). The October shoot length values from SC might be underestimated due to shoot fragmentation. The longer shoots at SC were due to longer, rather than more, inter-

TABLE 1. *Biomass allocation (percentage) and root: shoot ratios (R:S) for four field populations of* Murdannia keisak. *Roots include primary and adventitious roots. Data for all plants for each harvest date and site were pooled (N = number plants sampled)*

Site	Harvest	% Allocation				R:S	*N*
		Leaves	Stems	Roots	Flowers		
NT	May	30.84	40.53	28.64	–	0.40	237
	Jun	27.59	48.02	24.39	–	0.32	73
	Jul	27.25	60.83	12.37	–	0.14	47
	Aug	29.00	57.55	13.44	–	0.16	50
	Sep	24.89	63.25	11.86	–	0.13	41
	Oct	16.67	51.81	4.82	26.71	0.05	120
FT	May	39.42	40.15	20.44	–	0.26	209
	Jun	30.00	47.14	22.86	–	0.30	297
	Jul	29.11	56.81	47.97	–	0.16	52
	Aug	28.67	61.82	9.51	–	0.11	62
	Sep	18.99	67.28	13.73	–	0.16	25
	Oct	13.75	65.82	6.45	13.99	0.07	47
IT	May	31.47	43.03	15.94	–	0.34	1,414
	Jun	26.48	50.99	18.81	–	0.29	1,401
	Jul	26.68	40.14	16.59	–	0.50	1,115
	Aug	23.80	59.29	16.91	–	0.20	884
	Sep	15.29	71.40	10.43	2.88	0.12	649
	Oct	21.14	52.00	16.83	10.00	0.20	238
CT	May	28.96	42.07	28.97	–	0.41	1,345
	Jun	25.92	49.07	25.00	–	0.33	538
	Jul	27.88	55.62	16.50	–	0.20	703
	Aug	24.50	57.48	18.02	–	0.22	269
	Sep	14.65	73.27	9.11	2.97	0.10	616
	Oct	20.77	59.50	9.79	9.94	0.11	259

nodes: the mean number of nodes for SC plants (FT and NT combined; 16.2 ± 3.8 SD) and PB plants (CT and IT combined; 16.3 ± 1.9) did not differ significantly ($t = 0.105$, $P > 0.50$, df = 38).

In May, total stand biomass was similar at the PB and SC sites (Fig. 1c). By the end of the growing season, total stand biomass was significantly greater at the PB sites as a result of their greater density. SC plants increased rapidly in per plant biomass, peaking about 1 month earlier than PB plants (Fig. 1d). Because branches from FT and NT plants could become rooted late in the growing season and become established as new individuals, mean plant biomass in these populations declined in October. SC plants produced significantly ($t = 92.18$, $P < 0.05$) more branches (6.5 ± 1.3 SE) than PB plants (0.6 ± 0.3 SE). Separated branches can root and form new plants indistinguishable from parent plants, thereby increasing stand density and lowering mean plant biomass. Plants from the thermally disturbed sites (CT and IT) rarely branched until August, while FT and NT plants began branching in June.

The percentage of biomass allocated to shoots and roots did not differ significantly among the four populations. Throughout the growing season, a large percentage of the total plant biomass at both sites was aboveground (Table 1). At both sites, the ratio of root to shoot biomass (R:S) declined during the growing season. By October, biomass allocation to flowers was higher in SC than in PB populations and R:S was higher at PB.

Size hierarchies—Analysis of biomass distributions of plants from the two extremes of the thermal disturbance gradient (CT and NT) revealed both growth stage and population differences (Fig. 2). In May, the CT population was dominated by relatively small individuals (Fig. 2a) and differed significantly ($P < 0.05$ for Gini; CT > NT) from the NT sample (Fig. 2b) in which plant biomasses were distributed relatively evenly among size classes. By September, biomass dominance at both populations had shifted toward medium-sized individuals (Fig. 2c, d), although the relatively small Gini coefficients (G) indicate that a large fraction of the biomass was distributed more equitably within each population. From May to September, G decreased slightly at CT and increased slightly at NT. Consequently, the September Gs for the populations were indistinguishable.

The mean mass of individual seeds collected in October 1986 was significantly greater for

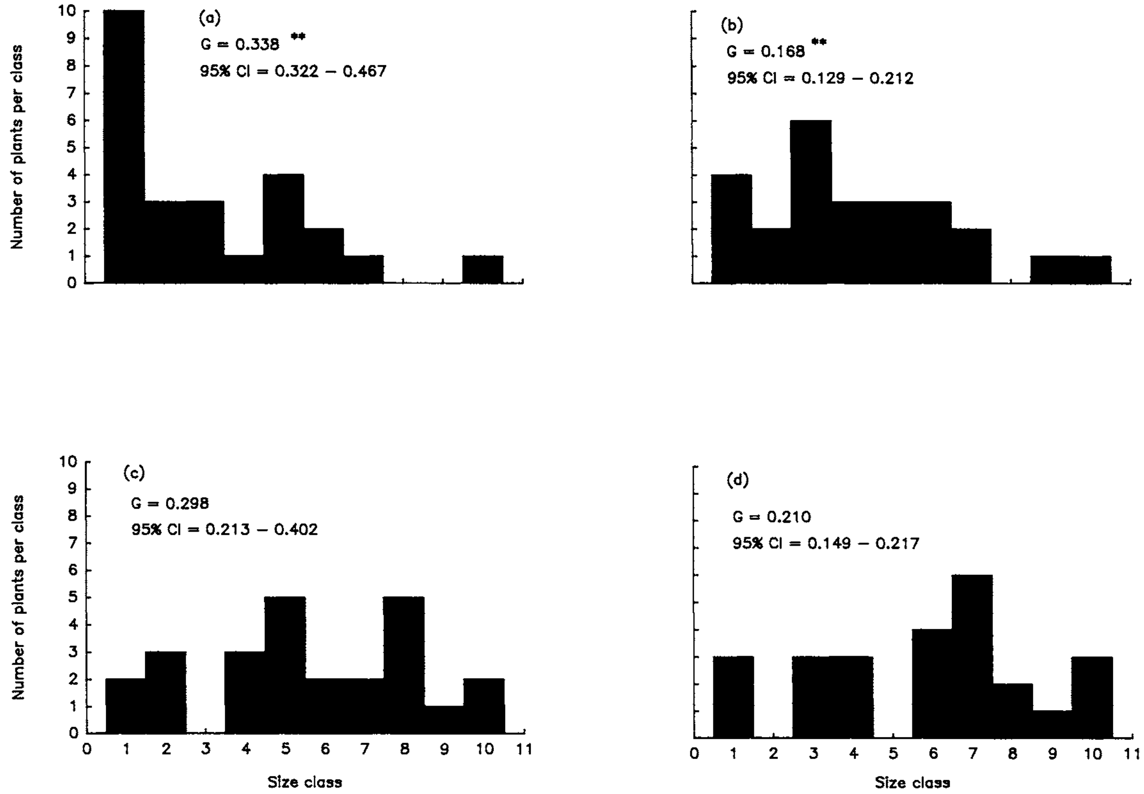

Fig. 2. Size hierarchies (plant biomass) of *Murdannia keisak* at (a) CT in May, (b) NT in May, (c) CT in September, and (d) NT in September. Gini coefficients and bootstrapped 95% confidence intervals are given for each size distribution. Distributions (a) and (b) differ significantly from each other (** = $P < 0.05$). No other differences are significant.

NT (3.94 ± 0.15 mg) than for CT (2.62 ± 0.17 mg) plants ($t = 5.7163$, df = 66, $P < 0.001$). Individual seed masses were significantly more variable at CT (CV = 38.33%) than at NT (CV = 23.58%) (log transformed; $F = 2.688$; $P < 0.05$). Furthermore, analysis of G showed that the distribution of seed mass was significantly less equal among CT plants than among NT plants (CT $G = 0.187$; NT $G = 0.130$; $P < 0.05$).

Reproductive effort and seed output—RE of both SC populations was generally greater than either PB population, regardless of which measure of RE was used (Table 2). Furthermore, there was a trend from higher RE in the undisturbed population (NT) to lower RE in the most disturbed (CT) population.

Comparisons of rankings using the October RE data from CT and NT plants indicated high correlations among the biomass ($RE_{1,2}$) and carbon- ($RE_{3,4}$) based measures of reproductive effort (Table 3). By contrast, the biomass and carbon-based measures were poorly correlated with the nitrogen measures ($RE_{5,6}$), suggesting that biomass can be an appropriate substitute for carbon, but not for nitrogen. All estimates of RE (Table 2) showed a significant concordance of ranks (Kendall's coefficient of concordance, $P < 0.05$; above and below the diagonal in Table 3). Thus, each of these mea-

Table 2. *Reproductive effort (RE) in four field populations of* Murdannia keisak. *Six definitions of RE are presented (see text for explanation). Steel Creek (NT and FT) populations did not flower in September. Pen Branch (CT and IT) populations flowered in both September and October*

	Date	Reproductive effort			
		NT	FT	IT	CT
RE_1	Sept	—	—	0.03	0.03
	Oct	0.39	0.18	0.14	0.12
RE_2	Sept	—	—	0.03	0.03
	Oct	0.27	0.14	0.10	0.10
RE_3	Sept	—	—	0.03	0.03
	Oct	0.30	0.15	0.12	0.11
RE_4	Sept	—	—	0.03	0.03
	Oct	0.29	0.14	0.10	0.10
RE_5	Sept	—	—	0.13	0.13
	Oct	0.38	0.30	0.37	0.29
RE_6	Sept	—	—	0.11	0.12
	Oct	0.37	0.28	0.30	0.25

TABLE 3. *Spearman rank correlations (significance level) among measures of reproductive effort (see text for definitions). Values above the diagonal are correlations between October harvests at Steel Creek and Pen Branch. Values below the diagonal compare Steel Creek RE (NT; October) with Pen Branch RE (CT) averaged for September and October*

	RE_1	RE_2	RE_3	RE_4	RE_5	RE_6
RE_1	–	0.95	1.00	0.95	0.80	0.80
	–	(0.05)	(0.00)	(0.05)	(0.20)	(0.20)
RE_2	0.95	–	0.95	1.00	0.63	0.63
	(0.05)	–	(0.05)	(0.00)	(0.37)	(0.37)
RE_3	1.00	0.95	–	0.95	0.80	0.80
	(0.00)	(0.05)	–	(0.05)	(0.20)	(0.20)
RE_4	0.95	1.00	0.95	–	0.63	0.63
	(0.05)	(0.00)	(0.05)	–	(0.37)	(0.37)
RE_5	1.00	0.95	1.00	0.95	–	1.00
	(0.00)	(0.05)	(0.00)	(0.05)	–	(0.00)
RE_6	1.00	0.95	1.00	0.95	1.00	–
	(0.00)	(0.05)	(0.00)	(0.05)	(0.00)	–

sures of RE might be describing the same reproductive allocation pattern and might be suitable for comparing RE among populations of *M. keisak.*

Seed output (fecundity) also differed among populations, with plants at both PB sites producing over 67,000 seeds per m², compared with about 9,000 produced by SC plants. This difference was due to both the greater plant densities (see above) and the significantly greater numbers of flowers per plant at PB sites (15.5 ± 2.5 SE) than at SC sites (10.2 ± 2.7 SE) ($t = 6.46$, $P < 0.05$). Average number of seeds per flower was similar between sites (3.3 ± 1.3 SE at SC, 3.1 ± 1.7 SE at PB; $N = 20$ plants per site).

Glasshouse plants*—Temperature and light treatments*—Most characters of plants grown from CT and NT seed appeared to be plastic in response to shade but not to any other treatment (Tables 4, 5). No interaction terms were significant. *F*-ratios (Table 4) for each treatment indicate that shade was the primary factor accounting for character divergence. Total number of branches, number of flowers, stem mass, flower mass, and total aboveground plant mass were all lower in shaded treatments (Table 5). Shoot length differed between shade treatments and between populations (there were no significant interaction terms in the experiments), suggesting that the differences may be due to both plasticity and to some genetic divergence between the populations. Although plants from both populations grew taller in shade (Table 5), shoot length was significantly higher for NT plants. The only character responding solely to temperature was leaf mass, which was greater in the high temperature treatment.

Reproductive effort (RE_1) of the glasshouse plants showed significant effects of both population and temperature (Table 4). The significant population term suggested that although both CT and NT plants responded in the same way to temperature, the RE of CT plants was consistently higher than that of NT plants (Table 5). As with shoot length, there might be some genetic divergence in these populations.

Water depth gradient—Results from the water depth gradient conformed to the dichotomy in plant growth form observed in the field (Fig. 3). For example, stem mass (Fig. 3a), leaf mass (Fig. 3b), and total plant biomass (Fig. 3f) decreased significantly with increasing water depth. The masses of other plant components were also related significantly to the water depth gradient (Fig. 3). For the sake of brevity, individual ANOVA tables are not presented; however, the patterns are evident from Fig. 3.

The water depth gradient was established to determine if PB (CT) plants were short in part because field water levels were lower than at SC (NT). Although mean shoot lengths did not differ significantly between flooded and deep treatments, there was a trend of increasing shoot length with increasing water depth (Fig. 3g).

TABLE 4. *Summary of three-way ANOVA results (with F-ratios) for the effect of population (P), temperature (T), and shade (S) on characters of two populations of glasshouse-grown* Murdannia keisak

Character	Pop	Temp	Shade	r^2	P
Shoot length	6.45*[a]	ns	69.22**	0.59	0.0001
Total no. branches	ns	ns	21.35**	0.34	0.003
No. flowers	ns	ns	117.20*	0.28	0.016
Stem mass	ns	ns	138.41*	0.76	0.0001
Leaf mass	ns	7.10*	ns	0.27	0.036
Flower mass	ns	ns	6.24*	0.17	0.248
Total mass	ns	ns	95.81**	0.68	0.0001
RE_1	5.62*	8.65*	ns	0.33	0.006

[a] * = $0.05 > P > 0.001$, ** = $0.001 > P > 0.0001$, ns = not significant ($P > 0.05$). r^2 and P are for the entire model. No interaction terms were significant.

TABLE 5. *Treatment and character means for two glasshouse populations of* Murdannia keisak: *(a) Steel Creek and (b) Pen Branch*

	Treatment[a]				
Character	AU	AS	HU	HS	$\bar{x}$
(a) Steel Creek (NT)					
Shoot length (cm)	134.68	169.75	131.37	171.45	147.95
No. main branches	9.25	12.00	10.60	8.83	10.17
Total no. branches	56.38	24.50	62.80	26.00	40.07
Stem mass (g)	23.58	8.76	21.93	7.83	17.57
Leaf mass (g)	3.22	2.73	4.07	3.49	3.46
No. flowers	250.75	99.17	244.40	73.17	182.80
Flower mass (g)	1.58	1.22	1.48	0.26	1.28
Reproductive effort	0.05	0.10	0.05	0.02	0.06
Total biomass (g)	28.38	12.70	27.48	11.58	22.30
(b) Pen Branch (CT)					
Shoot length (cm)	125.37	160.83	125.51	153.78	141.93
No. main branches	11.57	8.75	10.86	11.86	10.69
Total no. branches	81.14	29.43	51.57	28.71	47.71
Stem mass (g)	25.75	6.95	25.01	9.03	16.63
Leaf mass (g)	3.72	2.23	3.54	4.25	3.39
No. flowers	376.50	160.63	281.14	178.00	241.36
Flower mass (g)	2.76	1.26	1.98	1.01	1.74
Reproductive effort	0.07	0.12	0.06	0.07	0.08
Total biomass (g)	31.51	10.85	30.53	13.45	21.44

[a] Treatment AU = ambient water temperature and unshaded, AS = ambient with shade, HU = hot water and unshaded, HS = hot with shade. For significant effects, see Table 4.

PB plants formed many branches when not submerged (Fig. 3h). The flooded portion of this artificial gradient corresponded to field water levels at the PB sites. Nevertheless, branching was more profuse in the glasshouse than in either the PB or SC field populations.

DISCUSSION

There was little evidence that water temperature directly affected morphology and flower production in field populations of *M. keisak*. It appears that thermal pollution indirectly induced variability by killing overstory vegetation and increasing light levels. Glasshouse experiments suggested that much of the character divergence observed among field populations of *M. keisak* was apparently due to plastic responses to light conditions and water depth. The lack of significant interactions between population and temperature or light indicated no genetic differences in the plastic response among populations (Schlichting, 1986). Other common herbs on the same floodplain are sensitive to temperature. For instance, *Typha latifolia* displayed a plastic growth response to water temperature (Suda, Sharitz, and Straney, 1977), whereas seedling populations of *Ludwigia leptocarpa* showed a genetically fixed growth response to environmental temperature (Christy and Sharitz, 1980).

Although light had a significant effect on shoot length of glasshouse-grown plants, water depth also affected shoot length of *M. keisak* grown from CT seeds. Thus, in the field, the taller SC plants (NT and FT) could in part be a result of deeper water which promoted greater internode length. Water depth has been shown to promote greater internode length (and thus shoot length) in other aquatic plants, including *Oryza sativa* (Suge, 1987) and *Zizania aquatica* (Thomas and Stewart, 1969).

The glasshouse experiments did suggest some genetic divergence in shoot length and RE between field populations of *M. keisak*. For SC plants, there might be a trade-off between increased internode length (getting the shoot at or above the water) and flower number. For PB plants, this trade-off is less of an issue and more energy can be devoted to reproduction (L. F. Delph, personal communication).

Populations of *M. keisak* were more dense at both PB sites than at the SC sites, and these density differences could account for some of the phenotypic differences expressed among field populations. Populations at both sites experienced self-thinning (Dunn and Sharitz, 1990b); this density-dependent mortality could cause the changes in *G* noted for the CT and NT populations between May and September. Specifically, as the growing season proceeded, a larger proportion of smaller plants than larger plants died. Therefore, as self-thinning continued, populations became dominated by larger

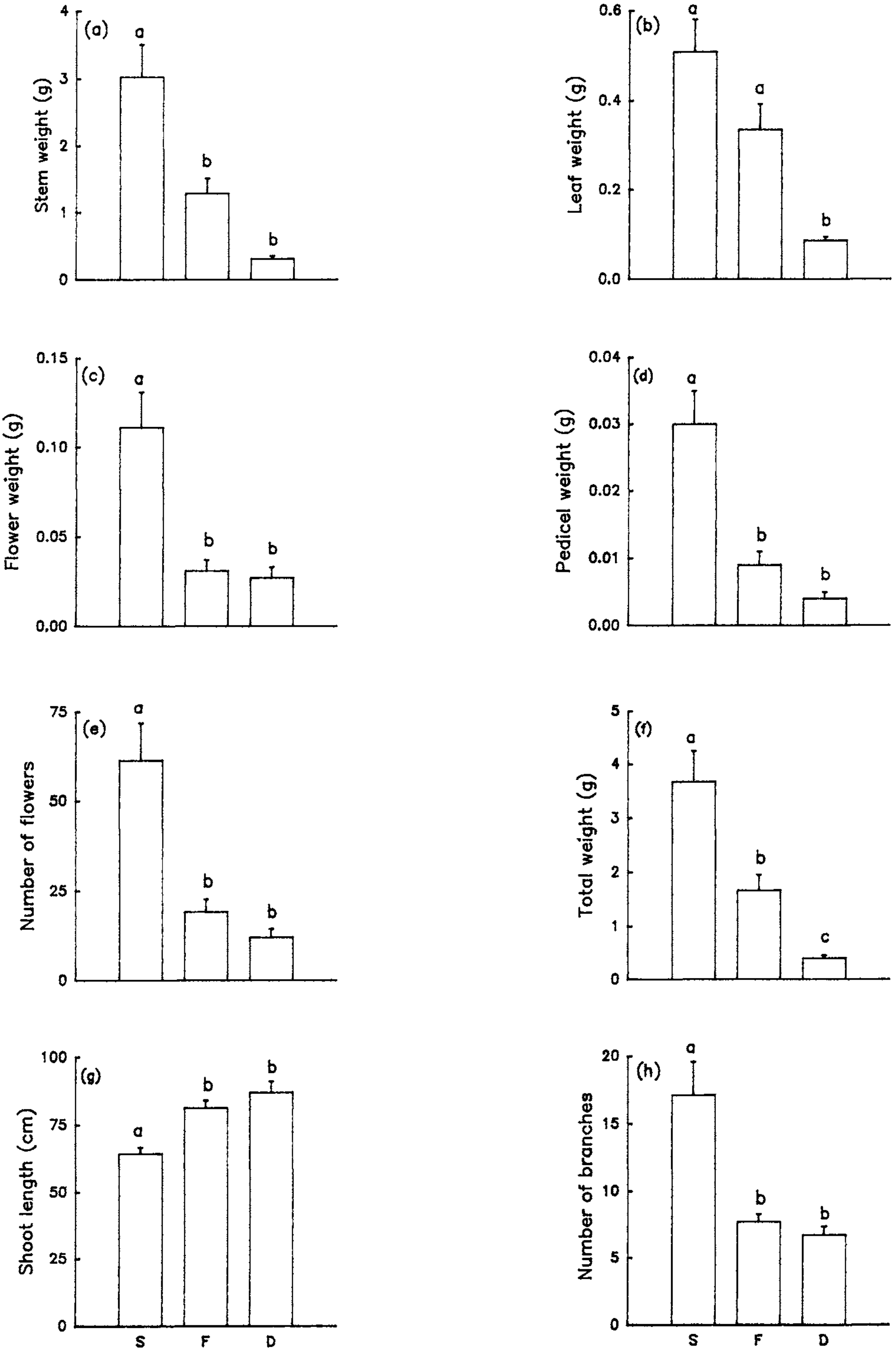

Fig. 3. Relationship of a water depth gradient for glasshouse grown CT plants to (a) stem mass, (b) leaf mass, (c) flower mass, (d) pedicel mass, (e) number of flowers, (f) total plant biomass, (g) shoot length, and (h) number of branches. Within each histogram, bars (mean ± 1 SE) denoted by the same lowercase letter do not differ significantly ($P > 0.05$) according to the Student-Newman-Keuls a priori multiple comparison test. S = saturated, F = flooded, D = deep-flooded.

plants, and *G* decreased (Weiner and Thomas, 1986).

Because PB field populations were more dense, PB plants produced appreciably more seeds per m^2 than SC populations. The mean individual mass of PB seeds was significantly lower than that of SC seeds. Mean seed mass within a species has been shown repeatedly to be remarkably constant (Harper, Lovell, and Moore, 1970; Salisbury, 1974), varying little despite documented plasticity of other organs (Fenner, 1985). This constancy has been interpreted as a homeostatic mechanism to maintain continuity between generations (Harper, Lovell, and Moore, 1970). Nevertheless, seed mass within some species does vary from site to site (Harper, Lovell, and Moore, 1970). For example, in populations of *Taraxacum officinale* (Solbrig and Simpson, 1974) and five species of *Solidago* (Werner and Platt, 1976), mean seed mass differed significantly among habitats. In open old-field communities, species of the perennial *Solidago* produced more and smaller seeds than the same species in mature prairie communities (Werner and Platt, 1976). Thus, there was a trade-off between seed number and seed mass related to the type of community in which the populations occurred (Werner and Platt, 1976). Variability in seed size might be adaptive because seeds of different sizes exploit different sites (Willson, 1983). Janzen (1978; as cited in Willson, 1983), for example, hypothesized that variability in seed size of some tropical species might permit more homogeneous dispersal of seeds around the parent plant, leading to a greater likelihood that some seeds will arrive at appropriate safe sites. Similarly, PB (open community) *M. keisak* plants produced more and smaller seeds than plants at SC (closed community).

Because glasshouse *M. keisak* plants were harvested before all plants had set seed, the differences in seed mass and number noted among the field populations could not be analyzed experimentally. However, flower number was obtained and was significantly affected by shade, but showed no population response (Table 4). Therefore, the field differences in flower number were probably a plastic physiological response to shade rather than fixed genetic differences. Furthermore, it did not appear that smaller seeds gave rise to smaller plants because there was no significant difference in biomass of PB vs. SC glasshouse-grown plants (Table 4).

In the field, greater seed output was found in the more dense *M. keisak* populations at PB. Harper (1977) speculated that crowded plants should reduce flower and seed production in response to density stress, perhaps because of a low availability of resources for seed production (Willson, 1983). On a unit area basis, then, total seed production should be similar in crowded and uncrowded populations. However, flower and seed production were higher per plant and per unit area in the high density PB populations. Increased seed production has also been described for crowded populations of the annual, *Polygonum cascadense* (Hickman, 1975).

Populations of annual plants in early successional or in light-saturated habitats can have higher RE (i.e., proportion of biomass or nutrients allocated to reproductive structures) than populations from shaded habitats (Hickman, 1975; Brown and Southwood, 1987). However, in field populations of *M. keisak,* higher RE occurred in the more shaded habitats of SC. These differences in RE, and the earlier flowering of PB plants, suggests some divergence in reproductive strategies between populations. Increased RE is related to increased size of many herbs (e.g., Christy and Sharitz, 1980; Weiner, 1988) as a result of increased number of flowers. However, this RE : flower number relationship is not the case for *M. keisak.*

Each measure of RE appears to describe the same allocation pattern. Thus, the easily determined biomass measures (RE_1 and RE_2) are suitable for comparing RE among populations of *M. keisak,* especially when comparing October estimates. All measures of RE were highly correlated when October values for SC were compared with averaged September values for PB. This relates in part to the methodological problem raised by Thompson and Stewart (1981); namely, the appropriate time to measure RE when different reproductive structures mature at different times. Thompson and Stewart (1981) also concluded that biomass measures are "inherently wrong in plants," but might be acceptable if a high correlation between biomass and nutrient measures can be shown, as for *M. keisak* (Table 3). Reekie and Bazzaz (1987b) state that it makes little difference which RE measure is used if relative differences in RE among populations are of primary interest, as was the case for these *M. keisak* experiments.

The variation (both plastic and genetic) in plant traits might allow individuals in each population to tolerate the different environmental conditions at each site. As the glasshouse results indicated, SC and PB plants showed some divergence with respect to reproductive effort and shoot length and both were plastic with respect to flower mass and number. Life-history, or reproductive, strategies themselves may be plastic, allowing plants to hedge their bets (Harper, Lovell, and Moore, 1970; Stearns, 1976; Dolan and Sharitz, 1984) or to switch strategies in disturbed environments (Solbrig and Simpson, 1974; Abrahamson, 1975a; Hickman, 1975; *M. keisak* in this study), under different population densities (Abrahamson, 1975b), in different successional stages (Roos and Quinn, 1977; Newell and Tramer, 1978; Stewart and Thompson, 1982), or from year to year (Soule and Werner, 1981).

Herbs have dominated the flora of the post-disturbance forested wetland near SC since 1968 (Sharitz, Irwin, and Christy, 1974; Dunn and Sharitz, 1987) and the disturbed areas near PB (Dunn and Scott, 1987). Why herbs continue to be dominant is unclear, but as this study and others (Suda, Sharitz, and Straney, 1977; Christy and Sharitz, 1980) suggest, the wide plasticity displayed by successional herbs may allow them to maintain dominance in varied and variable environments by increasing the number of tolerable habitats (Sultan, 1987) and thus effectively inhibiting the reestablishment of woody species.

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