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THE EFFECTS OF ULTRAVIOLET-B RADIATION AND INTRASPECIFIC COMPETITION ON GROWTH, POLLINATION SUCCESS, AND LIFETIME FEMALE FITNESS IN *PHACELIA CAMPANULARIA* AND *P. PURSHII* (HYDROPHYLLACEAE)[1]

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While a considerable amount of attention has been devoted to the effects that increased ultraviolet-B (UV-B) radiation has on vegetative plant growth and physiological function, the impact that UV-B may have on plant fitness has been the focus of fewer studies, with attention given primarily to a few crop species. Further, the possible interactions between UV-B and additional potential stresses found in natural environments have rarely been studied experimentally. Because the reported effects of increased UV-B on plant growth and fitness have been highly variable, studies that focus on factors that may lead to these differences in results are important for the formulation of accurate predictions about future plant success under varying UV-B levels. We examined the effects of UV-B dose and intraspecific competition on growth, phenology, pollen production, pollination success, fruit and seed production, and offspring quality in two species of *Phacelia*. Increased UV-B was neutral or beneficial for all traits, while competition was neutral or detrimental. There were no significant interactions between UV-B and competition in the parental generation. *Phacelia campanularia* offspring were unaffected by parental competition, but derived indirect beneficial effects on germination, growth, and fitness traits from parental enhanced UV-B.

Key words: fitness; growth; Hydrophyllaceae; intraspecific competition; *Phacelia*, pollination; ultraviolet-B; UV-B.

There is now little doubt that depletion of ozone in the Earth's stratosphere is occurring and that the amount of ultraviolet-B (UV-B) radiation reaching the surface of the Earth is therefore increasing (Frederick, 1993; Kerr and McElroy, 1993). Multiple deleterious effects of UV-B have been shown to occur in a wide variety of organisms (e.g., Jokiel, 1980; Dey, Damkaer, and Heron, 1988; Blaustein et al., 1994; Bothwell, Sherbot, and Pollock, 1994; Gieskes and Buma, 1997) including higher plants (Caldwell, Teramura, and Tevini, 1989; Krupa and Kickert, 1989; Bornman and Teramura, 1993; Runeckles and Krupa, 1994; Caldwell et al., 1995). However, relatively little work has been done specifically on the possible impact of enhanced UV-B levels on fitness (Teramura, 1990; SCOPE, 1992) although data on fitness effects are crucial to develop an understanding of potential population level responses to increasing UV-B radiation (Caldwell, Teramura, and Tevini, 1989).

Although fruit and seed yields of a few crop species have been examined in various studies (e.g., Teramura, 1990; Teramura, Sullivan, and Lydon, 1990), little research has focused on the effects of UV-B radiation on the fitness of plants from natural populations. Nor have many studies examined the possible impact of UV-B radiation on ecological factors that might themselves influence the fitness of a species, such as pollination success (SCOPE, 1992), interactions among neighboring conspecifics, or community-level interspecific interactions (but see Gold and Caldwell, 1983; Barnes et al., 1988; McCloud and Berenbaum, 1994; Grantpetterson and Renwick, 1996).

Increased UV-B could affect plant fitness in a number of ways. Ultraviolet-B has often been shown to reduce plant vegetative growth or inhibit photosynthesis (reviewed in Caldwell, Teramura, and Tevini, 1989; Fiscus and Booker, 1995), thus reducing the resources available to the plant for reproduction. Alternatively, it could affect pollination success by altering the ability of the plant to produce pollinator attractants (Conner and Zangori, 1997). A reduction in the number of flowers produced, for example, could potentially reduce pollinator visitation (e.g., Willson and Rathcke, 1974; Thomson, 1988; Eckhart, 1991; Conner and Rush, 1996). Even if pollinator visitation was not affected, reduced flower production could by itself lead to lower fruit set. Ultraviolet-B might also directly interfere with the ability of the plant to produce viable gametes or embryos by inducing deleterious mutations (Strid, Chow, and Anderson, 1994).

However, increased UV-B radiation does not always decrease fitness. At least one study (Feldheim and Conner, 1996) found that increased levels of UV-B usually resulted in enhanced female fitness in two species of *Brassica*, despite a known sensitivity to UV-B of other members of Brassicaceae (Van, Garrard, and West, 1976; Hashimoto and Tajima, 1980; Tevini, Iwanzik, and Thoma, 1981; Wilson and Greenberg, 1993). Additional studies on *Brassica* have suggested that these positive effects of UV-B may have been due to the reduced stress of the greenhouse environment (Conner and Zangori, 1997). Other experiments, however, have shown that enhanced levels of UV-B may be beneficial even in the presence of other environmental stress (e.g., Manetas et al., 1997).

Determining whether other stresses interact with UV-B in

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determining plant fitness requires manipulation of both, but most UV-B studies have manipulated UV-B alone. Most work on UV-B in concert with other stresses has examined water and/or nutrient stress. No interaction was found between UV-B and combined water and nutrient stress in *Brassica*, and the latter caused greater effects on fitness than UV-B (Conner and Zangori, 1998). Teramura, Sullivan, and Lydon, (1990) measured the effects of UV-B on seed yield and quality for six field seasons in two soybean cultivars. While water was not manipulated experimentally, they found that UV-B had its greatest effect on yield in wet years for the more sensitive cultivar, and only affected yield in the driest years for the other cultivar. Other studies have examined plant traits other than fitness, and either found no interaction between water/nutrient stress and UV-B (Bogenrieder and Doute, 1982; Teramura, Tevini, and Iwanzik, 1983) or found a specific interaction—water and nutrient stresses decreased the effects of UV-B (Teramura, 1986; Bornman and Teramura, 1993).

A major source of stress that could interact with UV-B is intra- or interspecific competition, but this competition is usually minimized or eliminated in greenhouse studies. Alterations in the architecture of competing individuals or species, which can occur under enhanced UV-B, may affect light interception and photosynthesis (Barnes et al., 1988; Barnes, Flint, and Caldwell, 1990; Ryel et al., 1990). Competitors could ameliorate the damaging effects of UV-B by blocking UV-B (Bogenrieder and Klein, 1982; but see Barnes et al., 1988), or they could enhance its effects by preferentially blocking the longer wavelength photosynthetically active radiation (PAR), which itself reduces the negative effects of the shorter wavelength UV-B (reviewed in Bornman and Teramura, 1993). Exposure to enhanced levels of UV-B radiation may affect competing individuals or species differentially in these and other ways, altering the competitive balance between them (Gold and Caldwell, 1983; Barnes et al., 1988). Thus, the magnitude and outcome of possible interactions between UV-B and competition are difficult to predict.

We tested for interactions between enhanced UV-B radiation and intraspecific competition in their effects on growth, phenology, pollination success, and female fitness in two species of *Phacelia*. Although the experiment was conducted primarily in the greenhouse, pollination was performed by an array of natural pollinators in the field. In order to assess lifetime female fitness, total flower, fruit, and seed production were recorded. Effects of parental competition and UV-B exposure on the next generation were estimated as offspring germination success, growth, and flower, fruit, and seed production. To our knowledge, this study and a related study (Sampson and Cane, 1999) are the first to examine the effects of UV-B in the Hydrophyllaceae.

MATERIALS AND METHODS

Experimental design—*Phacelia purshii* and *P. campanularia* (Hydrophyllaceae) are annuals native to the United States. *Phacelia purshii* is found in woods and fields of the north-central United States; seeds used in this study were collected from a natural population in Vermillion County, Indiana. *Phacelia campanularia* occurs in arid areas of the western United States. Seeds were derived from natural populations and purchased from the Theodore Payne Foundation (Sun Valley, California, USA). Three hundred *P. purshii* were planted in the greenhouse on 5 May 1996, and 240 *P. campanularia* on 10 June 1996. Due to incomplete germination and seedling mortality, final sample sizes were 130 *P. purshii* and 230 *P. campanularia*. All plants were grown in 7.5-cm pots in a 1 : 1 : 1 peat, perlite, and soil mixture. Plants were watered twice per day. Weekly fertilization to provide 237 ppm nitrogen was begun 26 July. To control aphids, all plants were sprayed with insecticidal soap weekly starting on 3 September.

Ultraviolet-B and intraspecific competition were manipulated in a 2 × 2 factorial design for each species. One-half of each species was randomly assigned to an enhanced UV-B treatment and the other half to a control UV-B treatment. Plants assigned to the control UV-B treatment received an ''ambient'' level of UV-B between 3.5 and 9.5 $kJ \cdot m^{-2} \cdot d^{-1}$ as the experiment progressed, mimicking seasonal variation in natural levels of UV-B at a 40° N latitude on a completely clear day. These represent current levels of UV-B calculated with the model provided by Green, Cross, and Smith (1980) and estimate the biologically effective dose according to the plant-damage spectrum of Caldwell (1971). Enhanced UV-B plants received an additional 11 kJ of supplemental UV-B per day over and above the control plant dose, so it varied between 14.5 and 20.5 kJ to mimic seasonal variation. These amounts of UV-B represent a level of ozone depletion that is more severe than the maximum expected according to most projections (e.g., Stolarski et al., 1992) and would require up to a 45% destruction of the ozone layer in middle latitudes (Green, Cross, and Smith, 1980). Ultraviolet-B levels were measured with an SED 240 radiometer (International Light, Newburyport, Massachusetts, USA) connected to a data logger (LI-1000, LI-COR, Lincoln, Nebraska, USA). The radiometer was calibrated with a UV/VIS spectroradiometer (Optronics OL 752, Optronics Lab, Orlando, Florida, USA). All UV-B measurements were conducted with the radiometer at the average leaf height of the plants. All UV-B treatments were begun when the first plants germinated and continued through senescence. Supplemental visible light was provided by 4–6 1000-W metal halide lamps per treatment group.

The UV-B radiation was provided by racks of 10 or 12 UV-B lamps suspended over the greenhouse benches. The UV-B lamps were covered with cellulose acetate of 0.0076 cm thickness for plants in the enhanced UV-B treatment group or 0.013 cm for plants in the ambient UV-B treatment group to allow the heights of the lamp racks to be maintained at relatively equal levels between treatments. The heights of the racks were adjustable to allow delivery of the correct dose of UV-B. Cellulose acetate was used because it transmits UV-B but absorbs UV-C (Middleton and Teramura, 1993). Transmission of UV-B through cellulose acetate decreases with prolonged exposure to UV-B, an effect greatest in the first hours of exposure, and therefore all cellulose acetate used was solarized before use for 10 h to stabilize transmittance. Cellulose acetate was changed whenever the transmission of UV-B dropped to a level low enough to require the UV-B lamp racks to be lowered to less than ~15 cm above the tallest plant, which occurred every 10–12 d.

Mylar sheets (0.013 cm) were hung between treatment groups to prevent any overflow of UV-B radiation from the racks above each treatment group to other groups. Mylar blocks wavelengths below ~316 nm (Middleton and Teramura, 1993). Plants of all four treatment groups were evenly divided between two different rooms in the same greenhouse. Rooms were treated as blocks in the analysis. In order to minimize any effects of environmental differences between areas of the greenhouse used, the positions of the flats were rotated every day within each treatment group. In addition, the location of the enhanced and ambient treatment groups within each block was switched every 5 d.

For each species, one-half of the plants from each UV-B treatment were randomly assigned to a crowded treatment, and the other half to an uncrowded treatment. Plants in the crowded treatment were grown in pots in which one other plant of the same species was also present, for a total of two plants per pot. A focal plant was chosen in each pot; no measurements of nonfocal plants were made. All references to plants in the crowded treatments refer only to focal individuals. Plants in the uncrowded treatment were alone in their pots. Shading from plants in neighboring pots was minimized by spacing individual pots as widely as possible on the greenhouse benches.

Growth and flowering measurements—Germination date and the dates of first and approximate last flowering were recorded for each focal plant in *P. campanularia*; the flowering dates were missed for some of the *P. purshii*. Plant height, leaf number and width, and the number of open flowers were recorded ~1 mo after the first plant germinated and again 2 wk later. Sub-

TABLE 1. Repeated measures ANOVA results for growth and open flower measurements in *Phacelia campanularia*. These values are from models that also included block and all possible interactions. R^2 values for the models ranged from 0.58 to 0.81, and all were significant at $P < 0.0001$. Total $N = 230$. See Fig. 1 for means.

	Height		Leaf number		No. flowers open		Leaf width	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Date	295.22	<0.0001	319.95	<0.0001	92.86	<0.0001	44.34	<0.0001
UV-B	0.05	0.82	0.99	0.32	0.00	0.96	1.91	0.17
Crowding	5.59	0.02	29.98	<0.0001	18.32	<0.0001	42.01	<0.0001
Date × UV-B	1.96	0.10	0.00	0.98	0.41	0.80	5.09	0.02
Date × Crowding	2.98	0.02	22.43	<0.0001	7.63	<0.0001	0.36	0.55
UV-B × Crowding	0.01	0.94	1.17	0.28	2.59	0.11	1.70	0.19

sequently, only plant height and flower number were recorded due to time constraints, at ~2-wk intervals until the plants began to senesce. Because *P. purshii* germination was more prolonged than *P. campanularia* germination, the plants were not as uniform in age on the dates on which growth measurements were taken. Plant height was measured from the surface of the soil to the highest point of the plant, without any manipulation of the plants (for example, straightening bent or leaning stems). Only leaves that were healthy and at least half open were counted. Leaf width was measured as the width of the lowest completely green leaf at the widest part of the leaf.

Pollen production—The anthers of one newly opened flower were collected from each focal plant. For the *Phacelia* species used in this study, there is a clear change in anther appearance a short time after flower opening, probably signaling dehiscence (R. Neumeier, personal observation). This allowed only newly opened (predehiscent) flowers to be used for this estimation of pollen production. Because the plants were kept in a pollinator-free greenhouse, this method allowed a reliable estimate of total per-flower pollen production.

The anthers were dried in an oven and the pollen grains counted with a Coulter counter. Four counts of the pollen present were performed for each individual sample and the mean of these counts then used to obtain an estimate of per-flower pollen production. For details of this procedure, see Rush, Conner, and Jennetten (1995).

Pollination and pollinator visitation—All flowering individuals were transported from the greenhouse to an outdoor field site (the University of Illinois Phillips Tract natural area near Urbana, Illinois, USA) for pollination by an array of natural pollinators. Approximately equal numbers of plants from each of the four treatment groups were taken to the field each day on a rotating schedule, so that each plant was exposed to pollinators once every 4 d. Plants from enhanced and ambient UV-B treatments were placed 100 m apart in order to minimize transfer of pollen between them. Treatment groups were switched between these two locations each day.

Pollination observations were done from 20 July 1996 to 12 September 1996. This period encompassed virtually the entire *P. campanularia* and most of the *P. purshii* flowering periods. Each focal plant flowering during the observation period was observed once, for 10 min. A total of 192 *P. campanularia* and 71 *P. purshii* were observed. Observations alternated between enhanced and ambient UV-B treatment plants. Where possible without observing a plant more than once, one of these plants was from the crowded treatment and the other from the uncrowded treatment. During observation periods, the number and taxa of pollinating visitors were recorded.

Female fitness components—Total lifetime flower, fruit, and seed production were recorded for each focal plant. The total number of flowers was measured by counting the number of pedicels remaining on the plant after senescence and adding the number of fruits collected. Pedicels of flowers that set fruit were removed from the plants as the fruits were collected. Fruits were collected as they matured and dried; once dried, the fruits were opened and the seeds removed, weighed, and counted.

Offspring germination and fitness—Twenty plants from each treatment group of *P. campanularia* (total = 80), approximately half from each block, were randomly selected as parents for progeny studies. Two randomly sampled seeds from each maternal parent were planted in a single pot and grown in the greenhouse without UV-B lamps. Offspring of parents from different crowding and UV-B treatments were interspersed on the greenhouse bench. The same was done for all *P. purshii* plants that successfully produced seeds; however, germination success was so low for this species that no usable data resulted from this experiment. Following the germination of offspring, seedlings were randomly thinned to one per pot. For all offspring results, crowding and UV-B treatments refer to the treatment groups of the parent plants, not the offspring themselves, since the latter were raised under uniform conditions.

Germination dates were recorded for all seedlings that germinated. The height of the seedlings 3 wk after germination and at first flowering was recorded. Once they began flowering, *P. campanularia* offspring were hand-pollinated every 3 d, with each plant used as a pollen donor for the next plant in numerical order (using plant identification numbers). All pollinations were done using offspring from the same parental block, crowding, and UV-B treatment groups. Offspring fruits were collected as they matured and the seeds counted. Total lifetime numbers of flowers, fruits, and seeds produced per plant were recorded.

Analysis—In order to reduce the number of tests performed given the large number of traits measured, related traits were grouped together for multivariate analyses of variance (MANOVA) to test for effects of UV-B, crowding, and their interaction. Separate univariate ANOVAs were performed on individual traits only if the MANOVA tests for any of these predictor variables were significant at the $P \leq 0.10$ level. The exceptions to this were the twice-monthly growth measurements (height, number of leaves, leaf width, and number of flowers), which were analyzed using univariate repeated-measures ANOVA only. Ultraviolet-B, crowding, and block were modeled as fixed effects in all analyses, which were performed using JMP (SAS, 1994). These MANOVA and ANOVA models included all interactions with block as well, but these are not shown for simplicity.

Pollinator visitation analyses also included a categorical variable for week to correct for temporal variation. Three multiplicative fitness components were analyzed for both parents and offspring: the number of flowers produced per plant, the number of fruits produced divided by flower number (percentage fruit set), and the number of seeds per fruit. Plants with zeroes for one or both of the first two components were not included in estimates of the subsequent components. These three fitness components multiply to equal the total number of seeds produced per plant, or lifetime female fitness.

RESULTS

In *P. purshii*, there were no significant effects of UV-B, crowding, or their interaction in the repeated measures growth analyses (data not shown). Ultraviolet-B had little effect on the growth of *P. campanularia*, with only a modest date × UV-B interaction for leaf width: there were no differences in leaf width at the first measurement and a small increase in width with increased UV-B at the second measurement (Fig. 1 and Table 1). In contrast, crowding caused strong reductions

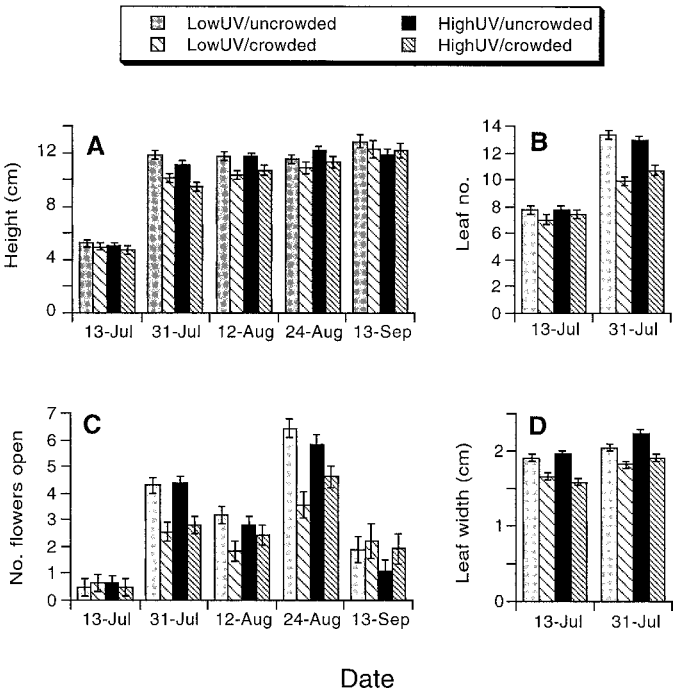

Fig. 1. Growth and flower production results (means ± 1 SE) for *P. campanularia*. See Table 1 for statistical tests and sample sizes.

in growth for all traits (Fig. 1 and Table 1; crowding main effect always significant), and these reductions were strongest at the intermediate dates for all traits except leaf width (date × crowding interactions). The strong date main effects for all traits indicate only that the plants were growing over time.

Neither UV-B nor crowding had significant effects on germination time or time from germination to flowering, but enhanced UV-B caused a delay in cessation of flowering in both species, increasing flowering duration (Tables 2 and 3 and Fig. 2A). In parallel with the growth results, crowding had a much stronger effect on lifetime female fitness and its components than did UV-B. Ultraviolet-B caused marginally significant increases in total flower production in *P. purshii* (Fig. 2B and Table 3) and in percentage fruit set in *P. campanularia* (Fig. 2C and Table 2). Crowding caused strong decreases in flower production in both species and seed production in *P. campanularia*, as well as a modest decrease in seed production in *P. purshii* (Fig. 2D and Tables 2 and 3). Neither UV-B nor crowding influenced pollen production in either species, but crowding produced small decreases in pollinator visitation in both species (Tables 2 and 3).

Seeds of *P. campanularia* parents grown under enhanced UV-B levels experienced greater germination success than those of parents grown under ambient UV-B levels (Table 4 and Fig. 3A). The resulting offspring of enhanced UV-B plants grew taller and produced more leaves and more seeds per fruit than the offspring of ambient UV-B plants (Table 4, Fig. 3B-D). Total female fitness, that is, lifetime seed production, was greater in the offspring of parents grown under enhanced UV-B, but only in the uncrowded treatment (Table 4, Fig. 3E). The lack of an effect in the crowded treatment is due in part to a marginally significant reduction in flower number with increased UV-B (Table 4, UV-B × crowding interaction for flower number). Except for these two interactions, crowding did not affect offspring fitness.

DISCUSSION

This study was designed to examine the effects of UV-B and interactions between UV-B and intraspecific competition on growth and fitness in two wild species of *Phacelia*. The results were primarily negative—while competition had strong detrimental effects on growth in *P. campanularia* and fitness in both species, there were few significant direct effects of UV-B and no significant interactions between UV-B and competition in the parental generation. This is surprising based on the large UV-B doses used and shows that *Phacelia* is quite tolerant to UV-B. In contrast, the results for the *P. campanularia* offspring showed several indirect effects of UV-B, but no effects of competition with the exception of one interaction with UV-B. All the effects of UV-B seem to be beneficial, with increases in flowering duration, total flower number, and percentage fruit set in the parental generation, and increases in germination, height, leaf number, seeds per fruit, and total seed production in the offspring.

In other studies that have tested for interactions between UV-B and other plant stresses, all possible results have been

TABLE 2. *Phacelia campanularia* parental MANOVA and ANOVA results. MANOVA was conducted for the three phenology traits and the five fitness traits; results from individual ANOVAs for these traits are indented below each MANOVA. Number of pollinator visits and number of pollen per flower were not grouped for MANOVA, so only ANOVA results are shown. R^2 and the significance level is for whole model; for MANOVA, the value of Wilks' λ is given instead of R^2. Flowering time is days from germination to first flower, and duration is days from first to last flower. #$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

			UV-B dose		Crowding		UV-B × crowding	
	λ or R^2	N	F	P	F	P	F	P
MANOVA: Phenology	0.68****	226	3.12	0.03	1.42	0.24	0.75	0.52
Germination time	0.14****	230	2.26	0.13	0.51	0.48	1.64	0.20
Flowering time	0.18****	227	1.53	0.21	0.55	0.46	0.03	0.86
Flowering duration	0.06#	226	7.08	0.008	1.93	0.17	0.63	0.43
No. pollinator visits	0.39****	192	2.57	0.11	4.49	0.04	0.04	0.84
No. pollen/flower	0.25****	195	1.86	0.17	0.13	0.72	0.44	0.51
MANOVA: Fitness	0.51****	218	0.82	0.55	4.05	0.002	1.28	0.27
No. flowers	0.09**	222	0.79	0.38	13.65	0.0003	0.13	0.72
Fruit set (%)	0.07*	222	4.88	0.03	0.22	0.64	2.52	0.11
Seeds/fruit	0.21****	221	0.40	0.53	0.04	0.83	2.78	0.10
Total no. seeds	0.24****	224	1.72	0.19	12.23	0.0006	0.12	0.72
Mean seed mass	0.11***	222	0.30	0.59	0.59	0.44	0.25	0.62

TABLE 3. *Phacelia purshii* parental MANOVA and ANOVA results. Differences in sample size are due to some variables not being recorded for all plants and plants with no fruits being eliminated from seeds/fruit. See Table 2 for details.

			UV-B dose		Crowding		UV-B × crowding	
	R^2	N	F	P	F	P	F	P
MANOVA: Phenology	0.51***	72	5.98	0.001	2.56	0.06	0.03	0.99
Germination time	0.17**	130	0.76	0.38	0.01	0.93	0.47	0.49
Flowering time	0.21**	101	2.40	0.12	1.67	0.20	1.04	0.31
Flowering duration	0.22*	72	6.12	0.02	2.78	0.10	0.03	0.86
No. pollinator visits	0.50*	71	0.14	0.71	4.12	0.05	0.06	0.81
No. pollen/flower	0.12	51	0.01	0.91	0.59	0.45	0.00	0.97
MANOVA: Fitness	0.50**	82	1.72	0.15	3.17	0.02	0.83	0.51
No. flowers	0.19***	124	3.70	0.06	11.02	0.001	1.30	0.26
Fruit set (%)	0.06	123	0.38	0.54	3.14	0.08	0.29	0.59
Seeds/fruit	0.02	103	0.03	0.86	0.01	0.92	0.01	0.93
Total no. seeds	0.08	130	0.00	0.97	4.22	0.04	0.06	0.80
Mean seed mass	0.15#	86	0.59	0.45	1.48	0.22	3.09	0.08

found. Some have found greater effects of UV-B on growth in the presence of other stresses (Bogenrieder and Doute, 1982; Teramura, Sullivan, and Lydon, 1990), and others have reported reduced effect of UV-B with other stresses (Murali and Teramura, 1986; Teramura, 1986; Sullivan and Teramura, 1990; Teramura, Sullivan, and Lydon, 1990; Bornman and Teramura, 1993). Two other studies have found a lack of interaction between UV-B and other stresses (Teramura, Tevini, and Iwanzik, 1983; Conner and Zangori, 1998). Thus, whether or not UV-B interacts with other stresses seems to depend on the species studied, the other stresses imposed, and experimental methods.

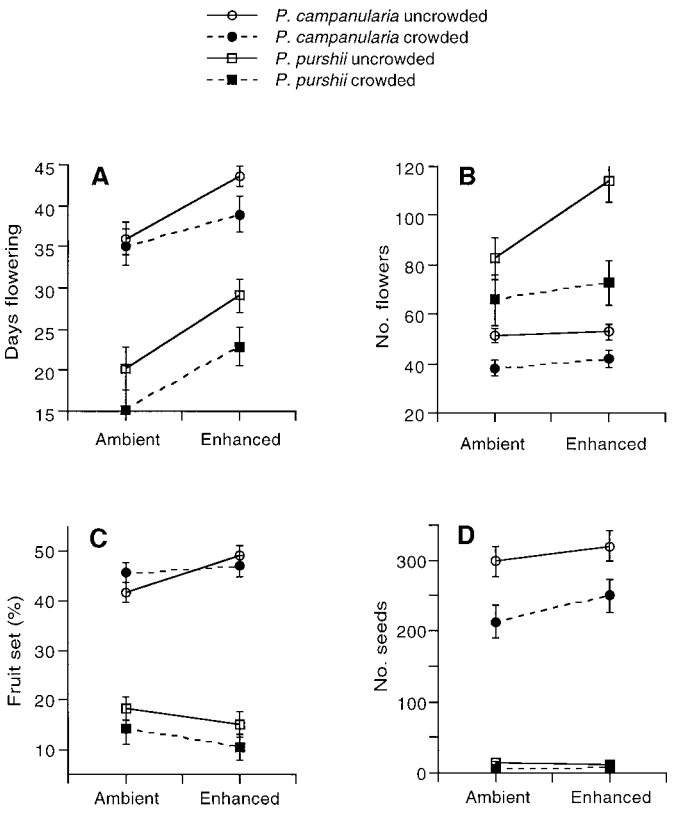

Fig. 2. Phenology and fitness components results (means ± 1 SE) for the parental generation. Only traits for which at least one treatment factor was significant at $P \leq 0.05$ are presented. See Tables 2 and 3 for statistical tests and sample sizes.

Studies looking specifically for an interaction between UV-B and competition have also reported variable patterns. Fox and Caldwell (1978) reported some evidence for interactions, in which both inter- and intraspecific competition increased the effects of UV-B in some of the species examined. Gold and Caldwell (1983) found an interaction between UV-B and interspecific competition, but no interaction with intraspecific interaction. When found, these interactions may be caused by UV-B induced changes in plant architecture (e.g., Barnes, Flint, and Caldwell, 1990; Ryel et al., 1990). Barnes et al. (1988) suggest that interactions between interspecific competition and UV-B are more likely than with intraspecific competition, due to the greater variability in architecture between species relative to within species. These ideas are consistent with our finding of no interaction between intraspecific competition and UV-B in the parental generation.

The effects of UV-B on plant productivity and fitness also appear to be idiosyncratic. Two recent reviews suggest that there is little evidence for negative effects under field conditions (Fiscus and Booker, 1995; Rozema et al., 1997), and while the majority of studies of fitness or crop yield report negative effects, there are a number that report no effect or even positive effects (Krupa and Kickert, 1989; Teramura, 1990; Teramura, Sullivan, and Lydon, 1990; Musil, 1995; Feldheim and Conner, 1996; Conner and Zangori, 1997; van de Staaij et al., 1997; Conner and Zangori, 1998). In the only other study that we know of that measured UV-B effects on fitness (seed production) in plants derived from natural populations without artificial selection, Musil (1995) found increased seed production in three of four monocot species studied and decreased seed production in three of four dicot species.

Our study was the first to measure the effect of UV-B on lifetime female fitness in the Hydrophyllaceae, and we found no significant effects on seed production in either species and positive effects on offspring quality in *P. campanularia*. The only other study to examine UV-B effects in this family found decreased lifetime flower production in *P. campanularia* grown in the greenhouse, in contrast to our study (Sampson and Cane, 1999). It would be interesting to see if the neutral or positive effects of UV-B on fitness that we found in the greenhouse also held in the field; positive or neutral effects of

TABLE 4. *Phacelia campanularia* offspring MANOVA and ANOVA results. The phenology MANOVA included germination and flowering times. Fitness analyses did not include the three-way interaction (UV-B × crowding × block) due to only a single replicate in one of the cells. Reductions in sample sizes are due to lack of germination or survival. See Table 1 for details.

			UV-B dose		Crowding		UV-B × crowding	
	R^2	N	F	P	F	P	F	P
MANOVA: Phenology	0.83	60	0.09	0.91	1.28	0.29	0.74	0.48
MANOVA: Growth	0.33**	60	2.26	0.04	1.71	0.15	2.70	0.03
No. germinating	0.17*	80	5.01	0.03	0.00	0.96	1.85	0.18
Height at 20 d	0.13	62	4.47	0.04	0.93	0.34	0.07	0.79
Height at flowering	0.24*	60	9.19	0.004	0.09	0.77	1.93	0.17
No. leaves at 20 d	0.18	62	5.35	0.02	0.05	0.82	1.38	0.25
No. leaves at flowering	0.20#	60	8.05	0.007	0.21	0.65	2.15	0.15
MANOVA: Fitness	0.39#	44	3.81	0.01	0.43	0.78	1.46	0.24
No. flowers	0.17	44	0.61	0.44	0.68	0.42	2.99	0.09
Fruit set (%)	0.08	44	0.66	0.42	0.56	0.45	0.39	0.54
Seeds/fruit	0.34*	43	14.44	0.0005	0.00	0.99	0.27	0.61
Total no. seeds	0.26#	43	6.68	0.01	1.45	0.24	6.25	0.02

UV-B on fitness in greenhouse *Brassica* studies (Feldheim and Conner, 1996) became neutral or negative effects when tested in an outdoor garden (Conner and Zangori, 1997). Another important area for future study is estimates of genetic variation for fitness-related traits under increased UV-B (e.g., Torabinejad and Caldwell, 2000).

To our knowledge, the only other studies that have measured the effect of UV-B on pollinator attraction are our previous studies on *Brassica*. Two of those reported similar results to the study reported here, i.e., no effect of UV-B on the numbers of pollinators visiting the plants (Feldheim and Conner, 1996; Conner and Zangori, 1998). In another study, increased UV-B increased visitation in one species and decreased it in another (Conner and Zangori, 1997); this was the only one of these experiments conducted on plants growing outdoors.

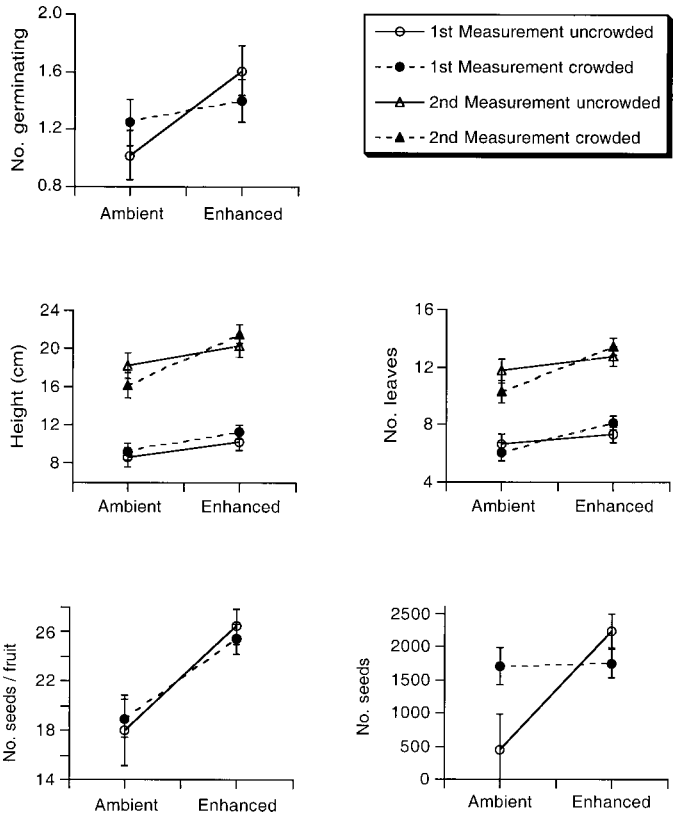

Fig. 3. Offspring growth and fitness results (means ± 1 SE) for *P. campanularia*. Only traits for which at least one treatment factor was significant at $P \leq 0.05$ are presented. See Table 4 for statistical tests and sample sizes.

As in this study, most previous research has found no UV-B effect on pollen production (Feldheim and Conner, 1996; Conner and Zangori, 1997, 1998; Sampson and Cane, 1999; but see Demchik and Day, 1996). In contrast to the lack of effect on pollen quantity, UV-B often decreases pollen quality, with negative effects on pollen germination and fertilization in many species, but not all (Flint and Caldwell, 1984, 1986; Musil, 1995; Demchik and Day, 1996; Conner and Zangori, 1997, 1998; Torabinejad et al., 1998).

The beneficial effects of UV-B on our offspring generation were caused by mutation, maternal effects, epigenetic inheritance, or effects of UV-B on the seeds, because the offspring plants were not exposed to enhanced UV-B or competition. Since most mutations are deleterious, it seems likely that the beneficial effects of UV-B we found are due to maternal effects or effects on the seeds. Perhaps the maternal plants, even though they do not themselves show the effects of UV-B, invest more in their offspring in the presence of enhanced UV-B. Note that this possible investment is not reflected in differences in seed mass, because seed mass did not differ among UV-B treatments (Table 2). Alternatively, the positive effect on offspring could be due to direct irradiation of the seeds; Musil (1994) reported such a positive effect in *Dimorphotheca* (Asteraceae). However, the seeds in our experiment were exposed to UV-B only while there were still in the fruit, whose thick walls would likely block most UV-B (Caldwell et al., 1995). To our knowledge, little is known about the impact of UV-B on epigenetic effects on plant fitness, but changes in genomic imprinting could potentially produce beneficial effects (e.g., Cubas, Vincent, and Coen, 1999; Wolffe and Matzke, 1999).

The lack of effects due to deleterious mutations may be due to the plants' natural screening and repair mechanisms (reviewed in Caldwell et al., 1995; Rozema et al., 1997), or they may be due to the single generation of UV-B exposure in our study. Musil (1996) found evidence for effects of deleterious mutations in a multigenerational study of UV-B exposure. Studies of these kinds of multigenerational effects, while difficult, represent one of the most important areas for future research on the effects of UV-B.

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