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COMBINED EFFECTS OF WATER, NUTRIENT, AND UV-B STRESS ON FEMALE FITNESS IN *BRASSICA* (BRASSICACEAE)[1]

JEFFREY K. CONNER[2,3,4] AND LAURA A. ZANGORI[2]

[2]Department of Ecology, Ethology, and Evolution, University of Illinois, Shelford Vivarium, 606 East Healey Street, Champaign, Illinois 61820; and
[3]Kellogg Biological Station and Department of Botany and Plant Pathology, Michigan State University, 3700 E. Gull Lake Drive, Hickory Corners, Michigan 49060

Our knowledge of the effects of increased levels of ultraviolet-B radiation (UV-B) on plant fitness is limited mainly to yield studies in a few crop species. Previous greenhouse and garden studies of *Brassica* have found greater detrimental effects of UV-B on fitness in gardens than in the greenhouse, suggesting the possibility that additional stresses in the field decrease the ability of *Brassica* to cope with UV-B. Possible interactions between UV-B and water/nutrient stress in determining plant fitness have rarely, if ever, been studied experimentally. Here we report measurements of female fitness in two species of *Brassica* in an experiment in which both UV-B and levels of water and nutrients were varied in a 2×2 factorial design. Water and nutrient stress reduced female fitness in both species, while UV-B caused fitness reductions in only one of the species. There was evidence for interactions between UV-B and water/nutrient stress for only a few of the traits measured; most traits, including those closely related to fitness, showed no evidence of an interaction.

Key words: *Brassica*; Brassicaceae; female fitness; global change; ozone destruction; ultraviolet radiation; UV-B; water and nutrient stress.

Due to the depletion of ozone in the earth's atmosphere, the amount of ultraviolet-B radiation (UV-B) reaching the earth's surface is increasing (Frederick, 1993; Kerr and McElroy, 1993). Ultraviolet-B has a wide range of deleterious effects on a variety of organisms (e.g., Jokiel, 1980; Dey, Damkaer, and Heron, 1988; Blaustein et al., 1994; Bothwell, Sherbot, and Pollock, 1994; McCloud and Berenbaum, 1994). A number of studies have examined the physiological and growth responses of plants to enhanced UV-B, and many of these have found damaging effects (see reviews by Teramura, 1983; Caldwell, Teramura, and Tevini, 1989; Krupa and Kickert, 1989; Tevini and Teramura, 1989; Bornman and Teramura, 1993; Runeckles and Krupa, 1994). However, the effects of UV-B on plant female fitness (defined as seed production) are less well known (Teramura, 1990; SCOPE, 1992). Ultraviolet-B may affect plant fitness in at least two ways. First, UV-B may cause mutations in pollen, ovules, or embryos (Jackson and Linskens, 1979; Strid, Chow, and Anderson, 1994). Second, UV-B can reduce growth and damage photosynthetic machinery (reviewed in Caldwell, Teramura, and Tevini, 1989); therefore, UV-B may cause fewer resources to be available for attracting pollinators and producing fruits and seeds.

In previous greenhouse studies, two species of *Brassica* actually increased lifetime seed production in response to increased UV-B in three out of four cases (Feldheim and Conner, 1996). In most published studies plant fitness declines or does not change in response to UV-B, but increases in yield with increased UV-B have been reported in a few crop species (reviewed in Feldheim and Conner, 1996); the reasons for these increases are unknown. However, when the same two *Brassica* species were exposed to increased UV-B under more stressful garden conditions, lifetime female fitness of one species declined and fitness of the other species did not change (Conner and Zangori, 1997). These results suggest that plants may be able to absorb increased UV-B without a fitness decline in the absence of other stresses, but that UV-B combined with other environmental stress may be detrimental. In contrast, studies of other plant species have suggested that water and nutrient stresses reduce the effect of UV-B on plant growth and physiology (Teramura, 1986; Bornman and Teramura, 1993; but see Bogenrieder and Doute, 1982; Teramura, Tevini, and Iwanzik, 1983). However, previous studies combining UV-B and water/nutrient stress have rarely measured fitness (but see Teramura, Sullivan, and Lydon, 1990). It may be that if plants are severely stressed by low water and/or nutrients, then fitness is already so low that differences in UV-B do not cause additional fitness reductions. When plants have ample water and nutrients, they may be able to compensate for, or protect themselves from, detrimental physiological effects of UV-B. However, there may be intermediate levels of water/nutrient stress at which the additional stress of enhanced UV-B causes additional reductions in fitness.

The goal of the study reported here was to test whether water and nutrient stress alters the effects of enhanced UV-B on total lifetime female fitness in *Brassica*. In addition, we hoped to determine the relative importance of

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[4] Author for correspondence (at Kellogg Biological Station).

UV-B vs. water and nutrients in determining fitness. To help determine the causes of any observed fitness differences, we measured growth, flower, pollen, ovule, fruit, and seed production, pollination success, and seed quality (seed size, germination success, and offspring growth).

MATERIALS AND METHODS

Rapid-cycling *Brassica nigra* (black mustard) and *B. rapa* (field mustard, canola, rape seed) were used for this experiment (Williams and Hill, 1986). The family Brassicaceae is known to be UV sensitive (e.g., Van, Garrard, and West, 1976; Tevini, Iwanzik, and Thoma, 1981), and these species have been used in related studies (Feldheim and Conner, 1996; Conner and Zangori, 1997). Both of these species are grown as crops and are also common weeds.

Experimental design—One-hundred and twenty plants of each species were planted in the greenhouse on 23 September 1994. Plants were grown in 7.5-cm pots in a 1:1:1 peat, perlite, and soil mixture. To control aphids, insecticidal soap was applied as needed until plants were 3 wk old; at this time, a single treatment of a systemic insecticide (Marathon; Olympic Horticultural Products) was applied. Supplemental visible light was provided by 1000-W metal halide lamps; average PAR (photosynthetically active radiation) during the light cycle was 552 $\mu mol \cdot s^{-1} \cdot m^{-2}$.

Thirty plants of each species were randomly assigned to one of four groups in a 2 × 2 factorial design, with UV-B as one factor and combined water and nutrient stress as the other. The two UV-B levels used were 6 and 17 kJ/m^2 UV-B_{be300}. Six kilojoules approximates current UV-B levels on a clear day on 1 June at 40° north latitude, according to a standard model (Green, Cross, and Smith, 1980). Seventeen kilojoules represents UV-B levels after ~45% destruction of the ozone layer. Ultraviolet-B lamps were illuminated for 6 h centered around solar noon daily from before plants germinated until senescence. For further details of UV-B delivery and measurement, see Feldheim and Conner (1996).

In the unstressed groups of the water and nutrient stress treatment, plants were watered twice daily, and fertilization to provide 237 ppm nitrogen was applied weekly. In the stressed groups, plants were watered only in the morning, with water given in the evening only to plants that were wilted or whose soil was dry. Fertilization to provide 59 ppm nitrogen was applied weekly. It is not known how these nutrient levels relate to those in the field, but *Brassica* generally grows in rich soils, and growth and reproduction decline in the greenhouse when fertilizer is reduced below the control amount (237 ppm; J. Conner, personal observation). Water and nutrient treatments began when plants produced their first true leaves and continued until senescence.

Plants were placed in 20 flats, with six plants of each species interspersed within each flat. Plants were well spaced in the flats to minimize shading; therefore, each plant is considered to be an independent experimental unit. Each flat was randomly assigned to one of the water/nutrient treatment levels, and flats were placed in rows with the two treatment levels alternating. The flats were rotated daily within UV-B treatment groups to reduce microenvironmental differences among flats.

Since only one pair of -B light racks was available, UV-B treatments were not replicated, but a number of steps were taken to ensure that differences between UV-B treatment groups were due to differences in UV-B itself (for further discussion, see Feldheim and Conner, 1996). First and foremost, every 5 d UV-B treatment groups were switched between racks, so that the light rack that had been 6kJ became 17kJ and vice versa. However, if there were other environmental differences between the benches under the two racks, and critical periods of plant development that lasted ≤5 d, it is possible that these other environmental factors could have caused differences between the UV-B treatment groups. To check for other environmental differences, PAR and temperature measurements were taken throughout the experiment at different hours and in a variety of weather conditions. There were no significant differences in conditions under the two UV-B light racks based on paired t tests (PAR: average difference 27.8 $\mu mol \cdot s^{-1} \cdot m^{-2}$, $t = 1.6$, $P = 0.14$, $N = 11$; temperature: average difference 0.1°C, $t = 0.4$, $P = 0.70$, $N = 4$).

Traits measured—*Growth and flowering phenology*—Growth and flower production were measured on all plants at weekly intervals from the development of the first true leaves to the cessation of flowering. The height of the plant, from the soil surface to its tallest point, was measured to the nearest 0.5 mm with a meter stick. All true leaves and open flowers were counted. In addition, the dates of first and last flowering were recorded and two traits were analyzed: the number of days from planting until the first flower opened, and the duration of flowering for each plant in days.

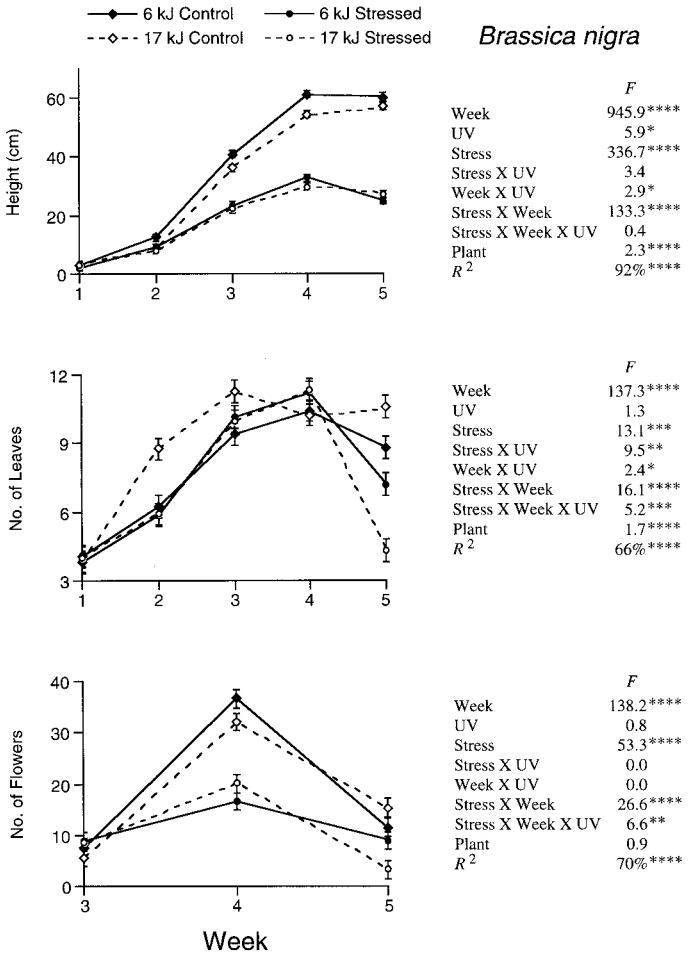
Pollinator attraction—To determine whether the treatments affected attractiveness of the plants to pollinators, observations of pollinator visitation were conducted in a 2.5-m^3 flight cage containing a small honey bee hive. Honey bees (*Apis mellifera)* were used because they are the dominant pollinators of *Brassica* worldwide (Fries and Stark, 1983). Each pollination trial used 30 plants from one UV-B treatment level, containing approximately equal numbers of the two species and stress treatments. Therefore, the bees were exposed to both species and both water/nutrient treatment groups simultaneously, which is a natural situation, but not simultaneously to plants exposed to two levels of UV-B radiation, which does not occur in nature.

All plants were exposed to bees for at least 30 min twice weekly. Plants were placed in a 5 × 6 grid on the floor of the cage. Two observers simultaneously observed one stressed and one unstressed plant of the same species for 10 min. During the next observation period a pair of plants from the other species was observed. The number of bees visiting, the duration of each visit, and number of flowers probed per visit were recorded. A total of 40 pairs of plants were observed, 20 pairs of each species.

Pollen and ovule production and pollen removal in B. nigra—One flower from each of 79 randomly selected *B. nigra* plants was removed for pollen and ovule counts. Ovules from a single flower from an additional seven plants were counted without pollen collection. An approximately equal number of flowers from each treatment group was collected on each day of sampling.

For the measures of pollen production, a newly opened flower was sacrificed and all six of its anthers placed in a clean vial. Because this flower opened in a pollinator-free greenhouse, this sample represented pollen production before any removal by pollinators. Thirty-three of these plants were exposed to honey bees immediately after pollen samples were collected. After pollination, the anthers of a flower adjacent to the flower sampled before pollination were collected. The number of pollen grains present in both samples was measured with a Coulter counter (for details see Rush, Conner, and Jennetten, 1995). The number of pollen grains removed by the bees was then estimated by calculating the difference in pollen counts between flowers collected before and after pollination (Harder, 1990; Young and Stanton, 1990; pollen production by adjacent flowers is similar in *B. nigra,* Feldheim and Conner, 1996).

Postpollination effects in B. rapa—To determine the effect of UV-B on pollen and ovule quality, hand pollinations were performed on *B. rapa.* Only flowers that had not been pollinated by bees were used. All crosses were done within UV-B dose and stress treatment groups, with approximately equal numbers of crosses done in each of the four groups on each day crosses were performed. Two flowers from different racemes were pollinated on each plant. A total of 78 plants were pollinated. Mature fruits were collected and the number of seeds produced counted.

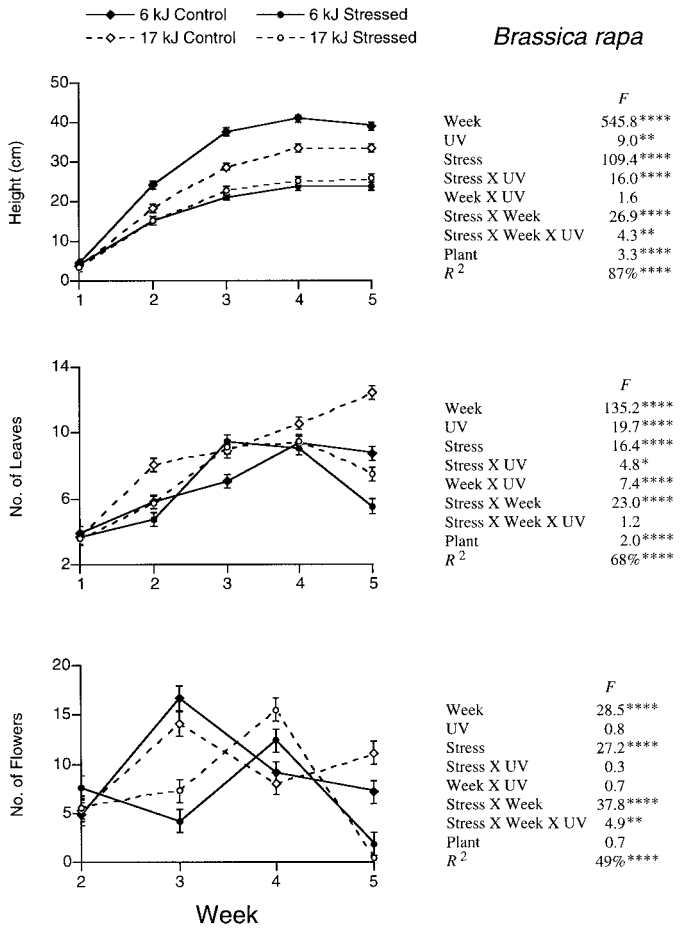


	F
Week	945.9****
UV	5.9*
Stress	336.7****
Stress X UV	3.4
Week X UV	2.9*
Stress X Week	133.3****
Stress X Week X UV	0.4
Plant	2.3****
R^2	92%****

	F
Week	137.3****
UV	1.3
Stress	13.1***
Stress X UV	9.5**
Week X UV	2.4*
Stress X Week	16.1****
Stress X Week X UV	5.2***
Plant	1.7****
R^2	66%****

	F
Week	138.2****
UV	0.8
Stress	53.3****
Stress X UV	0.0
Week X UV	0.0
Stress X Week	26.6****
Stress X Week X UV	6.6**
Plant	0.9
R^2	70%****

Fig. 1. Weekly growth and flower production results for *B. nigra* (means ± 1 SEM). ANOVA results for each trait are located to the right of each graph. $N = 115$ to 119 plants per week. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.



	F
Week	545.8****
UV	9.0**
Stress	109.4****
Stress X UV	16.0****
Week X UV	1.6
Stress X Week	26.9****
Stress X Week X UV	4.3**
Plant	3.3****
R^2	87%****

	F
Week	135.2****
UV	19.7****
Stress	16.4****
Stress X UV	4.8*
Week X UV	7.4****
Stress X Week	23.0****
Stress X Week X UV	1.2
Plant	2.0****
R^2	68%****

	F
Week	28.5****
UV	0.8
Stress	27.2****
Stress X UV	0.3
Week X UV	0.7
Stress X Week	37.8****
Stress X Week X UV	4.9**
Plant	0.7
R^2	49%****

Fig. 2. Weekly growth and flower production results for *B. rapa* (means ± 1 SEM). $N = 120$ plants per week. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

Fitness components—Plants were harvested upon senescence, air dried, and the following counts were made: total lifetime number of flowers produced (by counting pedicels), number of fruits, and total number of seeds. Air-dried fruits, seeds, and the rest of the aboveground plant were weighed separately. From these data, the following fitness components were calculated: number of flowers, number of fruits per flower, number of seeds per fruit (these multiply to equal total lifetime seed production), total aboveground biomass (fruit mass + stem mass), and reproductive effort (fruit mass divided by total aboveground biomass). Thirty-two seeds were then randomly sampled for offspring growth measurements.

Offspring measurements—To determine effects of UV-B exposure and stress treatments on offspring quality without confounding results with the direct effects of UV-B or stress on offspring, offspring were grown in a greenhouse in the absence of UV-B or water and nutrient stress. The randomly sampled seeds were planted in two 7.5-cm pots (16 seeds/pot) in Metro Mix 360 potting soil. Seeds from different UV-B doses, treatment groups, and species were interspersed within flats, with each flat containing four plants from each of the eight groups.

All germinating plants were counted and then seedlings were randomly thinned to one per pot. Two weeks (*B. rapa*) or three weeks (*B. nigra*) after planting, the number of true leaves were counted and plant height from the soil to the tallest part of the plant was recorded. These measurements were taken a second time on the day the plant first flowered.

Analysis—All statistical tests were conducted using JMP on Macintosh computers (SAS, 1994). UV-B dose and water/nutrient stress levels were treated as fixed effects. In most cases, related variables were grouped together and multivariate analyses of variance (MANOVA) were run to test for differences caused by UV-B and water/nutrient stress for the group of traits as a whole. If a multivariate test was found to be significant at $P \leq 0.05$, univariate ANOVAs were performed on each variable separately. Repeated-measures ANOVA was used to analyze the weekly growth measurements. Some dependent variables were ln-transformed to reduce heteroscedasticity.

RESULTS

Weekly growth measurements—Water and nutrient stress had a much greater effect on plant growth than UV-B in both species (Figs. 1, 2). In all cases the effects of stress varied among weeks, leading to interactions between these two variables. Both water/nutrient stress and enhanced UV-B caused plants to be shorter, but the effect of UV-B was only significant in the unstressed plants. The patterns for leaf and flower production are more complex. Surprisingly, the highest leaf numbers in both species occurred in the unstressed plants growing under

TABLE 1. Flowering phenology, fitness components, and offspring results for *B. nigra*. MANOVA results for groups of traits are listed first, with ANOVA results for individual traits indented below each significant MANOVA (see Methods). *F* values with significance levels are listed for UV-B, stress (water and nutrients), and UV-B × stress interactions. Wilks' lambda (MANOVA) or R^2 (ANOVA) with the significance level for whole model is listed in the last column.

Plant trait (dependent variable)	UV-B	Stress	UV-B × stress	Whole model
MANOVA (flowering phenology)	5.28**	4.72**	0.53	0.84**
Days to first flower	10.56**	9.52**	0.72	16%***
Flowering duration	0.30	0.68	0.13	1%
MANOVA (fitness components)	1.68	74.07****	2.95**	0.14****
No. of flowers	0.47	71.70****	0.00	39%****
No. of fruits/flower	0.81	64.82****	0.75	37%****
No. of seeds/fruit	0.01	26.22****	0.29	19%****
No. of seeds	1.28	190.02****	0.05	63%****
Average mass/seed	1.77	0.30	3.00†	4%
Total above-ground biomass	6.89**	404.54****	0.29	79%****
Reproductive effort	0.23	3.99*	0.07	4%
MANOVA (offspring traits)	0.73	1.87†	1.31	0.81

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

enhanced UV-B. There were not consistent differences among the other three treatment groups until the last week, when leaf number declined by differing amounts in these three groups while continuing to increase in the unstressed 17 kJ group. Ultraviolet-B did not affect weekly measurements of flower production, but water and nutrient stress caused significant reductions. This was particularly true in week 4 in *B. nigra* and weeks 3 and 5 in *B. rapa*. In the latter species, stressed plants actually had higher flower production in week 4, reflected in the strongly significant stress × week interaction.

Flowering phenology and fitness components—The MANOVA results for flowering phenology in both species show significant main effects of UV-B and stress, but no significant interaction (Tables 1, 2). In *B. nigra*, this is mainly due to stress causing earlier flowering and enhanced UV-B causing later flowering (Fig. 3A, Table 1). Conversely, in *B. rapa* the differences were mainly in flowering duration, with decreases due to stress and increases due to enhanced UV-B (Fig. 3B, Table 2).

There were no significant effects of enhanced UV-B on female fitness in *B. nigra*, except for a decrease in aboveground biomass (Fig. 3C–I; Table 1). In contrast, water and nutrient stress caused major reductions in all *B. nigra* fitness components except mass per seed. In *B. rapa*, enhanced UV-B increased lifetime flower production, but caused decreases in all other fitness components except mass per seed (Fig. 3C–I; Table 2). Water and nutrient stress decreased flower production, seed number and size, and aboveground biomass, but increased reproductive effort and the number of seeds per fruit in *B. rapa*. Note that there were no significant interactions between UV-B and stress, except in the MANOVA for *B. nigra* fitness components. Finally, the MANOVA analyses for offspring quality showed no effect of UV-B and a marginally significant effect of water and nutrient stress in both species (Tables 1, 2).

TABLE 2. Flowering phenology, fitness components, and offspring results for *B. rapa*. See Table 1 for details.

Plant trait (dependent variable)	UV-B	Stress	UV-B × stress	Whole model
MANOVA (flowering phenology)	6.24**	15.03****	2.72†	0.69****
Days to first flower	4.61*	0.65	5.45*	8%*
Flowering duration	10.00**	30.30****	0.05	26%****
MANOVA (fitness components)	4.15***	28.39****	1.38	0.30****
No. of flowers	11.44***	59.39****	0.58	38%****
No. of fruits/flower	23.44****	0.03	2.75	19%****
No. of seeds/fruit	7.20**	7.91**	0.52	12%**
No. of seeds	13.27***	9.02**	1.51	17%****
Average mass/seed	0.00	6.68**	1.99	7%*
Total above-ground biomass	7.63**	109.90****	0.05	51%****
Reproductive effort	3.42†	17.92****	1.98	17%****
MANOVA (offspring traits)	0.93	2.07†	1.25	0.80

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

Pollination success—Neither increased UV-B nor water and nutrient stress had a significant effect on pollen production, ovule production, or pollen removal in *B. nigra*, or pollinator visitation in both species (data not shown).

Hand pollination—The hand-pollination experiments showed that both water/nutrient stress and enhanced UV-B decreased seed production by affecting postpollination events (e.g., pollen performance, ovule quality, seed abortion; Fig. 4). However, the detrimental effect of UV-B occurred only in the stressed plants (significant stress × UV-B interaction).

DISCUSSION

In our experiment, water and nutrient stress had a much greater effect on the plants than did enhanced UV-B. Both enhanced UV-B and water/nutrient stress had detrimental effects on *B. rapa*, but the effect of the latter was much stronger. Water and nutrient stress also had large negative effects on *B. nigra*, while UV-B had little effect.

The most striking result of this study was the lack of interaction between UV-B and water/nutrient stress for most traits, particularly traits closely related to fitness. There were no UV-B × stress interactions for flowering phenology, fitness components, pollination success, or offspring quality. Therefore, this study does not help explain the differences between the garden and greenhouse environments in the response of *Brassica* to UV-B. There are several possible explanations for this. First, UV-B effects may not be repeatable across experiments. However, the results presented here generally corroborate our earlier greenhouse fitness results (Feldheim and Conner, 1996). In both studies, UV-B did not have a detrimental effect on female fitness in *B. nigra*, but did cause decreased fitness in *B. rapa*. Second, the amount of stress

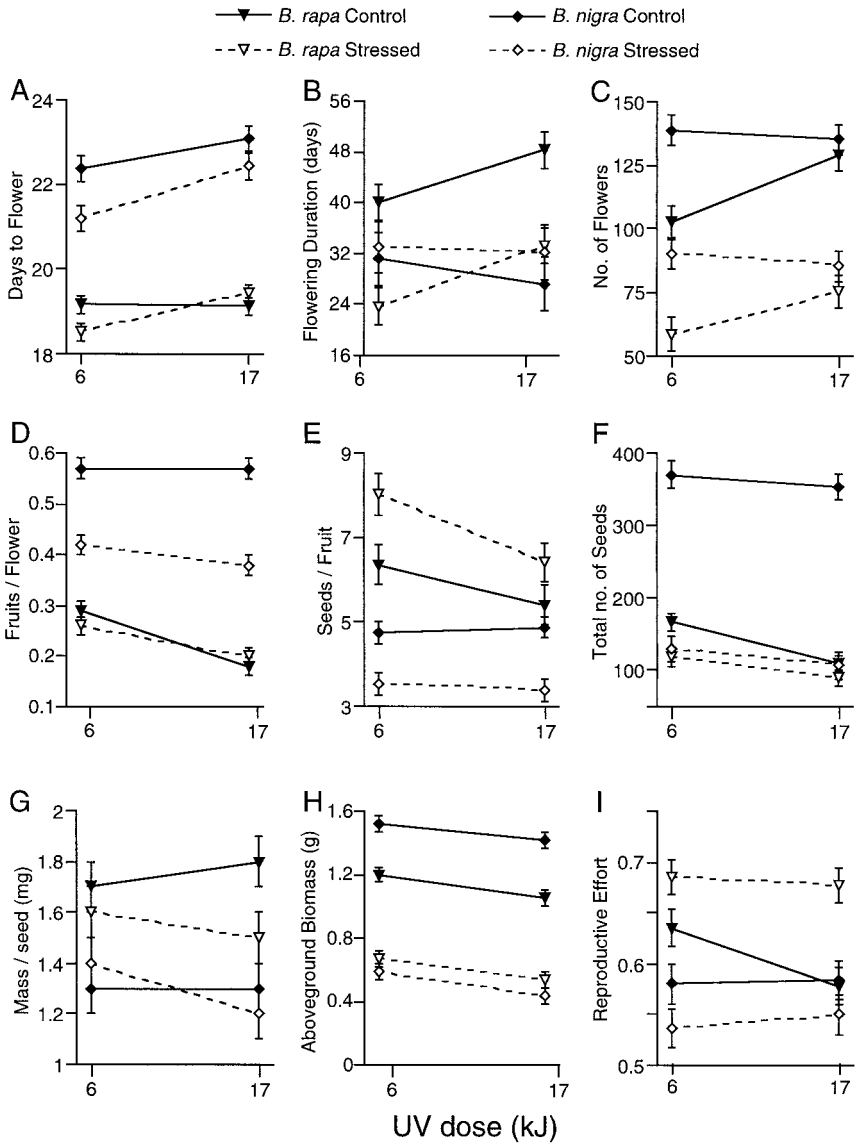


Fig. 3. Flowering phenology and fitness component results for both species (means ± 1 SEM). See Tables 1 and 2 for ANOVA results. N = 237 for days to first flower and number of seeds, N = 235 for all other traits.

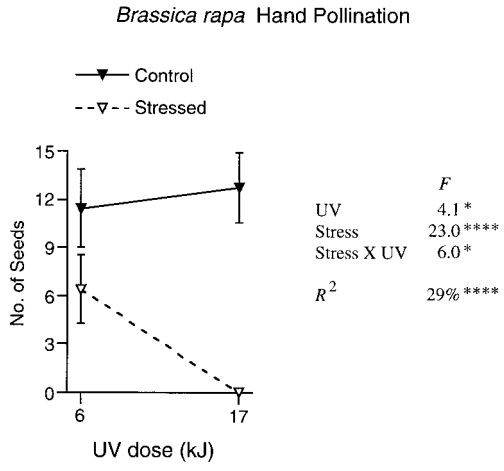


Fig. 4. Hand-pollination trial results (means ± 1 SEM). Total N = 78.

that we delivered may not have been representative of stress levels in the garden study. Plants in our garden study were watered and fertilized (Conner and Zangori, 1997), so perhaps the water/nutrient stress we delivered was more severe than in the garden study. Finally, there are many other sources of stress in the garden other than water and nutrients. The deleterious effects of UV-B are augmented by low PAR (reviewed in Bornman and Teramura, 1993), but this would probably cause less UV-B stress in the field. The effects of UV-B on plant attack by pests and pathogens are variable (McCloud, Berenbaum, and Tuveson, 1992; McCloud and Berenbaum, 1994; reviewed in Bornman and Teramura, 1993); although some pest control was used in both of our studies, this is a possible additional stress in the field. Clearly, more studies are necessary to resolve the discrepancy between garden and greenhouse results.

Most previous studies have found that detrimental ef-

fects of UV-B are masked when plants are under water and/or nutrient stress (Teramura, 1986; Bornman and Teramura, 1993; but see Bogenrieder and Doute, 1982; Teramura, Tevini, and Iwanzik, 1983). The only trait in our study that clearly fit this pattern was height: UV-B caused a reduction in height when plants were unstressed, but there was no UV-B effect when plants were water and nutrient stressed. This was certainly true in *B. rapa* and appears to be true in *B. nigra*, although in the latter the UV-B × stress interaction is not statistically significant.

The results of our previous studies on *Brassica* (Feldheim and Conner, 1996; Conner and Zangori, 1997) suggested a different UV-B × stress interaction: that UV-B might not decrease plant fitness when plants are unstressed, but does when plants have other stresses as well. The only results from our study that support this hypothesis were the hand-pollination data (Fig. 4): here, UV-B had no effect on unstressed plants but caused decreased seed production in stressed plants.

Another study of the effects of UV-B on reproduction in *B. rapa* found that increased UV-B decreased pollen production (Demchik and Day, 1996). In a total of four separate experiments, we have never found UV-B effects on pollen production in *Brassica* (*B. nigra*, this study; *B. nigra* and *B. rapa*, Feldheim and Conner, 1996; Conner and Zangori, 1997). In addition, honey bees showed no differences in behavior or amount of pollen collected when foraging for pollen on *Brassica* plants raised at different UV-B levels (Collins, Conner, and Robinson, 1997). Our studies were conducted using higher enhanced doses than those used by Demchik and Day, so it is unclear what caused the differences among studies. In the study reported here, we found increases in flower number with increased UV-B regardless of stress treatment in *B. rapa* (Fig. 3), similar to Demchik and Day (1996); however, in earlier work on *B. rapa* we found either decreases or no change in flower number (Feldheim and Conner, 1996; Conner and Zangori, 1997). One methodological difference between the studies is that we measured lifetime flower production while Demchik and Day measured the number of flowers open on one day.

In summary, the general lack of interaction between UV-B and water/nutrient stress found in this study suggests that these two factors may act fairly independently in *Brassica*. However, interactions between these stresses have been reported in other species (reviewed in Teramura, 1986; Bornman and Teramura, 1993), and results for *Brassica* may be different if this interaction was examined in the field or with different levels of UV-B and water/nutrient stress. More research will be needed to determine the generality of our finding of low interaction between these environmental stresses.

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