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COMPETITIVE INTERACTION IN PLANT POPULATIONS  
EXPOSED TO ENHANCED UV-B RADIATION

by

Fred M. Fox

A thesis submitted in partial fulfillment  
of the requirements for the degree  
of  
Master of Science  
in  
Range Ecology

Approved:

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Major Professor

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Committee Member

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Committee Member

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Dean of Graduate Studies

Utah State University  
Logan, Utah

1977

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*Fred M. Fox*

Fred M. Fox

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## ABSTRACT

Competitive Interaction in Plant Populations Exposed  
to Enhanced UV-B Radiation

by

Fred M. Fox, Master of Science

Utah State University, 1977

Major Professor: Martyn M. Caldwell  
Department: Range Science

Competitive balance and changes in individual plant growth parameters of eight pairs of plant species exposed to enhanced UV-B irradiation were determined under field conditions simulating ozone reductions of about 0.08 atm·cm. The levels of irradiance represented ozone decreases of about 25-30 percent from approximate ambient ozone concentrations for high solar altitudes on clear days during the study. A method for calculating and statistically analyzing relative crowding coefficients was developed and used to evaluate the competitive status of the species pairs sown in a modified replacement series. The effect of UV-B irradiance was generally detrimental to plant growth, and was reflected in decreased leaf area, biomass, height and density as well as changes in competitive balance for various species. For some species interspecific competition apparently accentuated the effect of UV-B radiation, while intensive intraspecific competition may have had the same effect for other species.

( 91 pages)

## INTRODUCTION

Ozone is concentrated in the upper atmosphere above 12 km and attenuates solar UV-B (280-315 nm) irradiance received at the Earth's surface. Global UV-B radiation flux varies with differences in solar angle, aerosol concentration of the atmosphere, cloudiness and changes in stratospheric ozone concentration. In temperate latitudes, virtually no UV-B radiation below 295 nm is received at the surface of the Earth at intensities greater than  $10^{-3} \text{ W} \cdot \text{m}^{-2} \cdot \text{nm}^{-1}$ . However, a reduction of stratospheric ozone would result in increased UV-B irradiation including some irradiance below 295 nm (Green, Sawada, and Shettle 1974). Ozone can be catalytically destroyed by nitrogen oxides released from aircraft traveling in the stratosphere (Grobeck, Coroniti, and Cannon 1974, Johnston 1971), chlorides produced by vehicles such as the space shuttle and halomethanes which diffuse up into the stratosphere (Cicerone, Stolarski, and Walters 1974). A moderate increase of global UV-B radiation might have substantial biological impact because both nucleic acids and proteins are active chromophores in the UV-B spectrum (Giese 1964). Damage caused by UV-B radiation is often subtle and may affect such plant processes as cytoplasmic streaming and photosynthesis (Caldwell 1971, Sisson and Caldwell 1976).

Most investigations of plant response to ultraviolet radiation have employed nearly monochromatic radiation (254 nm) from mercury vapor germicidal lamps. Radiation of this quality is not naturally



received by biological systems and would not occur even if stratospheric ozone concentrations were substantially reduced. With the sun directly overhead, a 90 percent reduction in ozone concentration from a base level of 0.30 atm·cm would still not result in ground-level irradiance below 280 nm of an intensity greater than  $10^{-3} \text{W} \cdot \text{m}^{-2} \cdot \text{nm}^{-1}$  (Caldwell 1977).

Caldwell (1971) has noted the difficulty in predicting damage to plant processes by UV-B radiation from results with monochromatic germicidal radiation. Consequently, UV-B radiation sources which can approximate the expected spectral irradiance should be used in studies assessing the potential biological impact of stratospheric perturbations.

Caldwell (1971) proposed a method for determining the biological effectiveness of UV-B radiation in phenomena involving protein and nucleic acid chromatophores. A generalized action spectrum was suggested (Caldwell 1971) which Green, Sawada, and Shettle (1974) formulated as follows:

$$\epsilon(\lambda) = 2.618 [1 - (\lambda/313.3)^2] e^{-(\lambda-300)/31.08} \quad (1)$$

For monochromatic irradiance the biologically effective UV-B irradiance ( $\text{W} \cdot \text{m}^{-2} \cdot \text{nm}^{-1}$ ) can be characterized as:

$$\text{UV-B}_{\text{BE}} = \epsilon_{\lambda} \cdot I_{\lambda} \quad (2)$$

where  $\epsilon_{\lambda}$  is the relative energy effectiveness of UV-B radiation as defined in equation 1 and  $I_{\lambda}$  is the irradiance ( $\text{W} \cdot \text{m}^{-2} \cdot \text{nm}^{-1}$ ). For polychromatic irradiance, the biologically effective irradiance

( $\text{W}\cdot\text{m}^{-2}$ ) can be determined by integrating over the appropriate waveband:

$$\text{UV-B}_{\text{BE}} = \int_{288}^{313} \epsilon_{\lambda} I_{\lambda} d\lambda \quad (3)$$

Integrating over time would yield the total dose ( $\text{Joules}\cdot\text{m}^{-2}$ ) of UV-B<sub>BE</sub>.

Damage caused by moderate UV-B irradiation is subtle and often difficult to detect in single plants grown in individual pots. In this study plants were grown under conditions of competitive stress which may augment the expression of the radiation damage. This method also provides competitive conditions for growth which are more representative of conditions experienced by plants in natural systems. Finally, this approach permits a better assessment of potential shifts in competitive balance in natural communities which might occur under increased UV-B irradiance.

Eight plant species pairs were chosen to represent competitive interactions encountered in actual field systems. Several criteria were used in the selection of the species pairs. Each competing pair represented a biologically meaningful association. Some attempt was also made to pair a species which might be sensitive to UV-B radiation with a species which might be resistant. Sensitivity to radiation at 254 nm (Cline and Salisbury 1965) was used to predict sensitivity to UV-B radiation, although there are problems associated with this procedure as previously stated. Table 1 is a list of the competing pairs of species studied which comprised three general ecological categories; agricultural crops and their associated weeds,

montane summer range species, and disturbed-area weedy associates. The timing of growth was considered and each species was paired with another species which normally grows at the same time of the season.

Plants appear to differ in their susceptibility to UV-B radiation, probably due to differences in leaf geometry, morphology, and repair capabilities. Because of this differential tolerance to UV-B irradiance, plant species might differ in the amount of injury or growth impairment which they incur. Consequently competitive ability could be influenced. Thus, the following hypothesis was proposed.

1. The competitive balance between species is altered by a moderate increase of UV-B radiation.

Abiotic stress factors such as nutrient deficiency, water stress and extreme temperatures might be expected to alter the expression of UV-B-induced damage or growth impairment. Herbivory, competition and other biotic factors could also influence the expression of UV-B damage in plants. Competitive stress is of particular interest since plants normally grow under this constraint in most natural and agricultural systems. Competitive stress could be expected to enhance the expression of UV-B injury.

To test this thesis, the following hypothesis was set forth:

2. If the UV-B insult is exacerbated by interspecific competitive stress, then elevated UV-B irradiance should have a greater effect under conditions of most severe interspecific competition.

If changes in competitive response actually occur under enhanced UV-B irradiation, they are probably the result of altered physiological processes. This should also be reflected in altered growth parameters of individual plants. Therefore, the third hypothesis to be tested was:

3. Enhanced UV-B irradiance will result in altered individual plant growth parameters.

If hypotheses 1 and 3 are supported, then a corollary hypothesis can be developed.

4. Since UV-B radiation is generally detrimental to plants, the growth of a species can appear to be enhanced, only as a result of UV-B radiation growth impairment of the competing species.

The study was designed to experimentally investigate the effects of supplemented UV-B irradiance on whole plant response in competing pairs of plant species grown in the field. A change in the competitive interaction between species of the pair was determined by measurements of changes in density and shoot production. Growth parameters of plant height, weight, and leaf area at time of harvest were also evaluated. Some species responded to enhanced UV-B irradiance and competitive stress with a depression in growth and the competitive balance between some species pairs was altered under increased UV-B irradiance.

## METHODS

Seeds from each competing pair were randomly sown in 10 cm x 10 cm pots using a modified DeWit replacement series (DeWit 1960). A constant total density of 50 seeds per pot was maintained, but the relative densities of the competitive species were varied. Three relative sowing frequency classes were used with five replicates of each. The classes were:

### Class

1	5 seeds cospecies 1: 45 seeds cospecies 2
2	25 seeds cospecies 1: 25 seeds cospecies 2
3	45 seeds cospecies 1: 5 seeds cospecies 2

Each pot was partially filled with a coarse screened potting soil mixture over which was placed 1-2 cm of finely screened mixture. The potting mixture contained two parts screened clay-loam and one part commercial potting soil. The mixture was then screened and sterilized. The seeds were randomly sown and covered with 1 cm of the fine screened potting mixture. Immediately after sowing in late July the pots were placed in field plots for the duration of the study. The pots were watered each morning to field capacity with an automatic individual pot watering system.

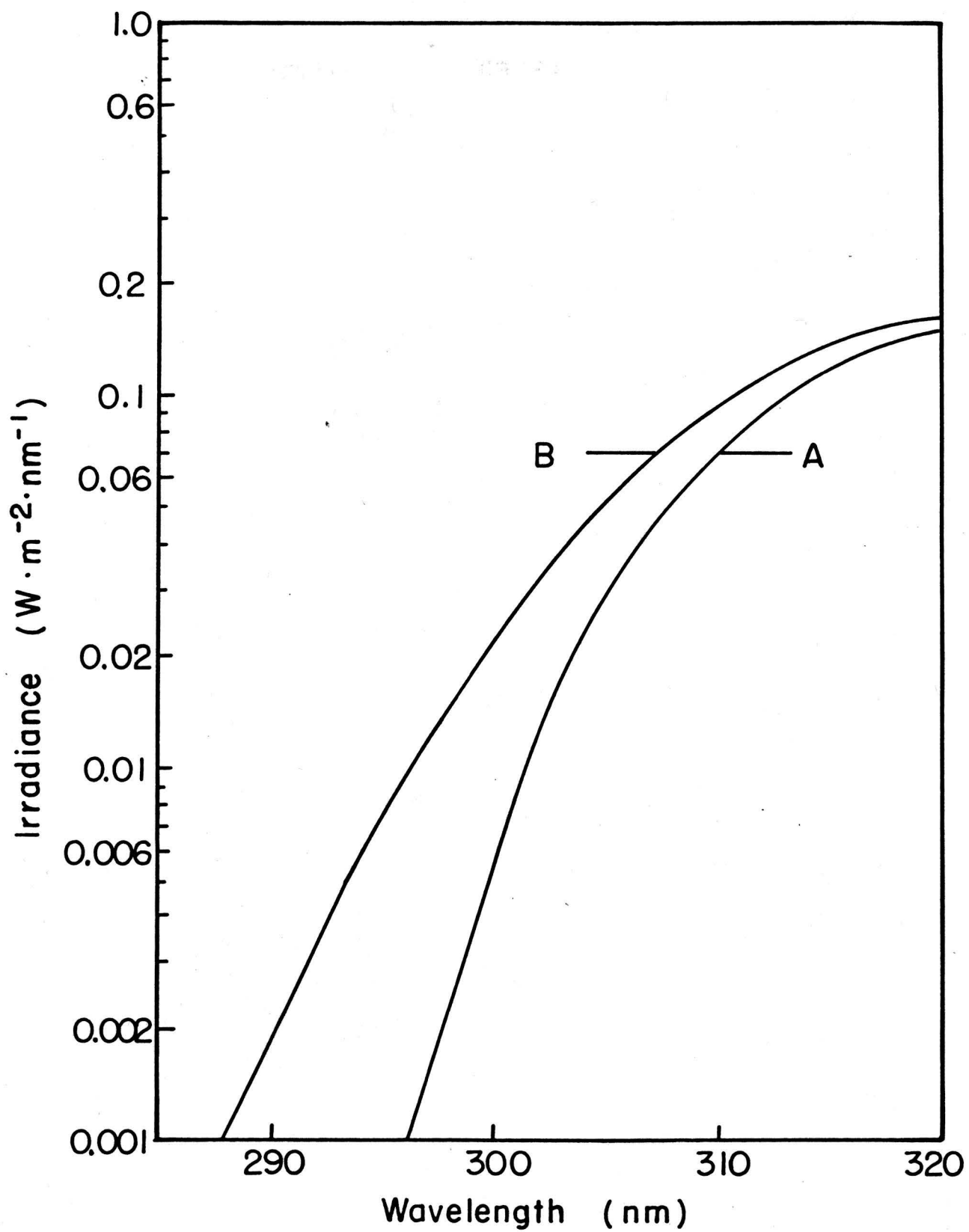
For seven hours each day centered about solar noon, UV-B radiation was supplemented with five filtered Westinghouse FS-40 "sunlamps" situated 43 cm above the pot rims. These fixtures directly irradiated a 120 cm x 120 cm area in which the pots were arranged in a 10 x 10 pot grid. The outer row of pots on each side was sown with

a mixture of Medicago sativa and Amaranthus retroflexus and left as an unsampled border. The outside row of pot had no neighbors on at least one side and an edge effect could develop due to differences in irradiation and wind movement. The unsampled border prevented the development of an edge effect. The remaining test pots were randomly reassigned new positions every three days to help reduce the effects of uneven irradiation and other microenvironmental differences.

The surviving density of each cospecies was determined at intervals during the growing season. At harvest in September and October all plants were individually clipped at ground level and shoot dry weight was determined after drying at 60°C. Shoot height and leaf area were determined for those species pairs for which it was feasible. Leaf areas were measured with a Lambda Model II-3000 area meter.

Two UV-B irradiance treatments were provided for all density classes of each competing species pair by using identical lamp fixtures with different plastic film filters. The lamps in the supplemented UV-B irradiance treatment were covered with one layer of Kodacel TA 401 (5 mil; 0.13 mm) (Kodak Co.) polyester film. Since this film solarizes and becomes more opaque to UV-B radiation, these filters were changed every three to five days. The lamps in the control treatment were covered with one layer of Mylar Type A (10 mil; 0.25 mm) (Dupont Co.) polyester film. Figure 1 shows the spectral irradiance of these two treatments for August 16 when the sun was at an angle from the zenith,  $\theta$ , of 37° and stratospheric ozone concentration was about 0.295 atm·cm (Hering and Borden 1967).







(At this time of year,  $\theta$  is  $28^\circ$  at solar noon. At  $\theta$  of  $37^\circ$ , the UV-B supplemented irradiance (curve B) corresponded to a 0.08 atm·cm decrease in stratospheric ozone calculated from the following equation (Sisson and Caldwell 1975).

$$Oz_2 - Oz_1 = \frac{\ln I_{m,\lambda} - \ln I_\lambda}{10 (1/\cos\theta)e^{(300-\lambda)/8}} \quad (4)$$

where  $Oz_1$  is the base ozone level,

$Oz_2$  is the reduced ozone level,

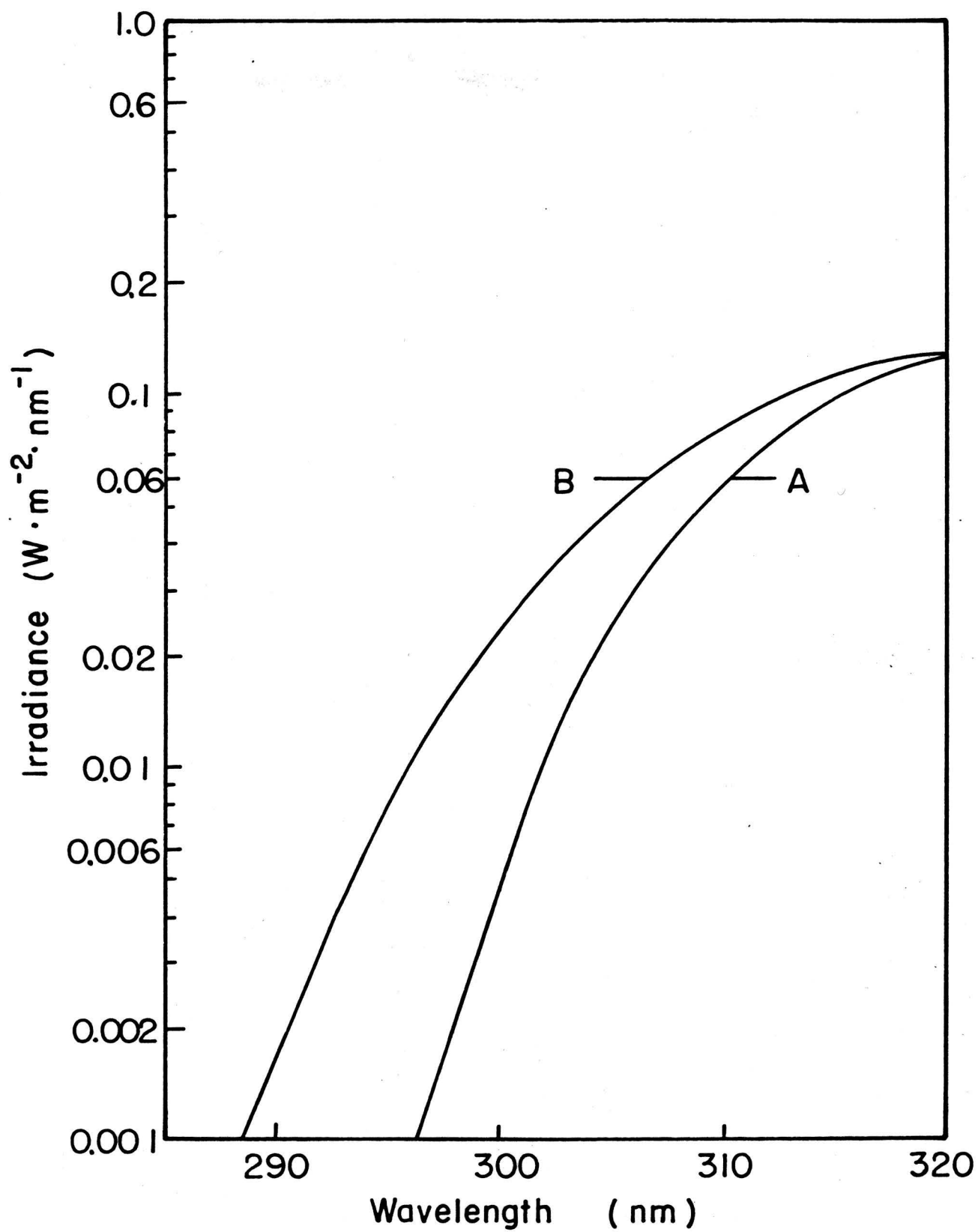
$I_{m,\lambda}$  is the global solar irradiance supplemented by the Mylar filtered lamp system,

$I_\lambda$  is the global solar irradiance supplemented by the Kodacel filtered lamp system,

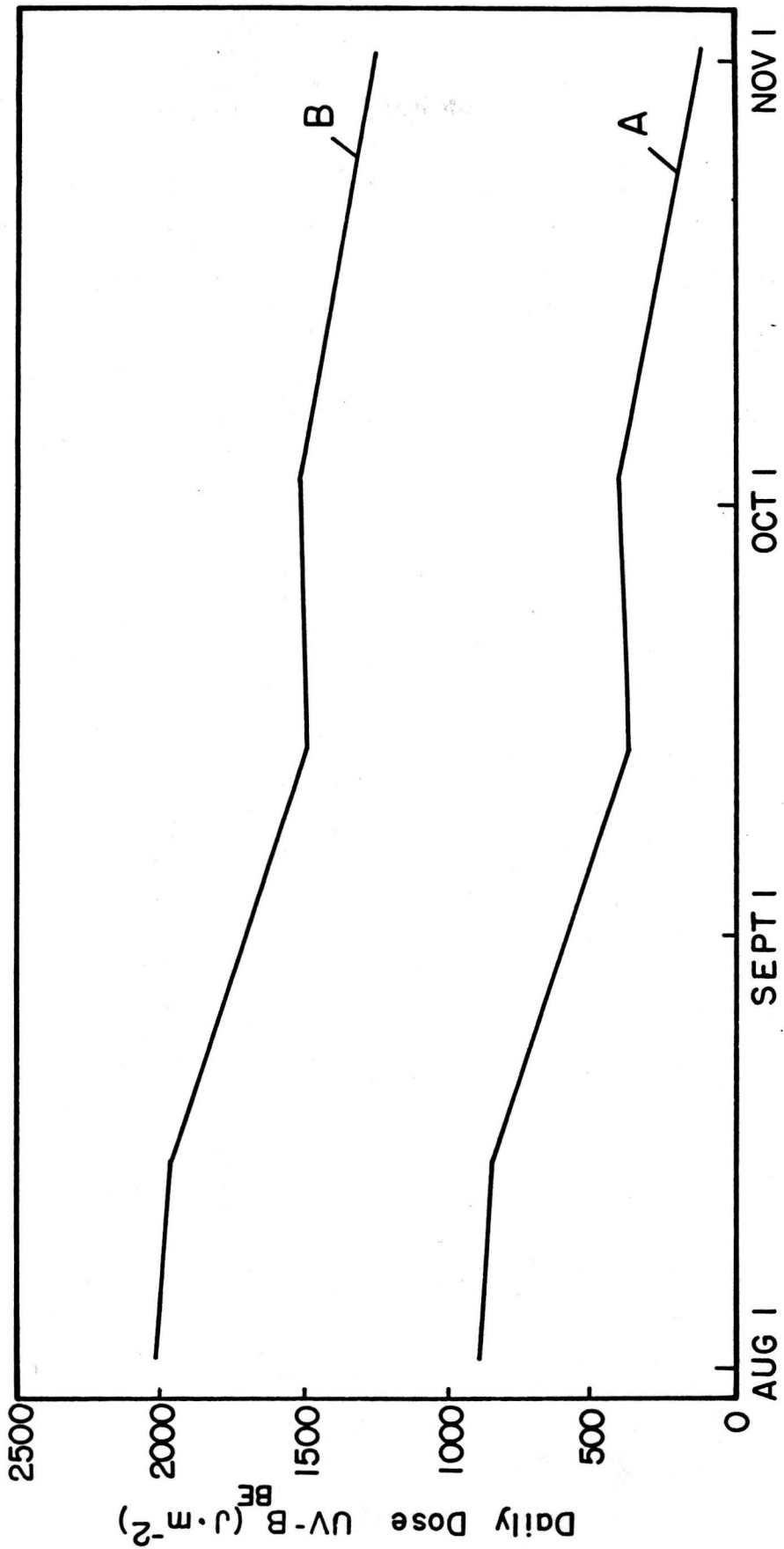
and  $\theta$  is the solar angle from the zenith.

This represented a 27 percent decrease in ozone from a base level of 0.295 atm·cm. Figure 2 illustrates similar data for noon ( $\theta = 46^\circ$ ) on October 3 when the normal ozone concentration was 0.27 atm·cm. This represented a 0.08 atm·cm decrease in ozone or a 30 percent decrease from the 0.27 atm·cm base level of ozone. The total daily dose of biologically effective UV-B irradiation during the growing season is shown in Figure 3. This was determined by integrating UV-B<sub>BE</sub> at half hour intervals over the 7 hour "day" of radiation supplementation. This represents over 90 percent of the total UV-B<sub>BE</sub> received during a 12-hour day. Since actual measurements of the spectral irradiance were made at only 1 or 2 different times on any given day, the values of UV-B<sub>BE</sub> for the remaining half-hour intervals were determined by the following procedure. The model of Green, Sawada, and Shettle (1974) for terrestrial UV radiation was used to









Date

Daily Dose UV-B ( $J \cdot m^{-2}$ )

compute  $UV-B_{BE}$  at values of  $\theta$  corresponding to half-hour intervals on dates when the spectral irradiance under the control (Mylar-filtered) lamp systems had been determined. Using the model of Green, Sawada, and Shettle (1974) the relative changes of irradiance from the value at  $\theta$  for the time of the measurement to the values at  $\theta$  for the remaining half-hour intervals were determined in order to predict the irradiance under the Mylar-filtered lamp system at these time intervals. This method gives reasonable values of  $UV-B_{BE}$  since there was a good correlation between the relative change predicted by the model and the actual relative change of the measurements at two different times in a day. Values of  $UV-B_{BE}$  throughout the day for the enhanced UV-B treatments were calculated by adding the radiation supplemented by the enhanced UV-B treatment lamps ( $0.0448 \text{ W}\cdot\text{m}^{-2} \text{ UV-B}_{BE}$ ) to the irradiance for the control lamps. These values were integrated over the day to provide the total daily  $UV-B_{BE}$  dose (biologically effective  $\text{Joules}\cdot\text{m}^{-2}$ ) for the two treatments.

#### Calculation of the competition parameters

The DeWit model of competition (DeWit 1960) evaluates competitive interactions by determination of the relative crowding coefficient,  $k_{12}$ , which is characterized by:

$$k_{12} = \frac{O_1}{Z_1} \cdot \frac{Z_2}{O_2} \cdot \frac{M_2}{M_1} \quad (5)$$

where  $Z_1$ ,  $Z_2$  are the number of seeds sown for species 1 and species 2, respectively, and  $Z_1 + Z_2 = \text{constant}$

$M_1$ ,  $M_2$  are the respective yields (e.g. dry matter, number of seeds produced) when species 1 and 2 are grown in monoculture,

and  $O_1, O_2$  are the respective yields when species 1 and 2 are grown in mixed stands.

By substituting the experimental values of  $M_1$  and  $M_2$  and  $O_1$  and  $O_2$  for each combination of seed sowing densities  $Z_1$  and  $Z_2$ , one or more values of  $k_{12}$  can be obtained. This value is substituted into the following equations:

$$A_1 = k_{12}z_1[k_{12}Z_1 + Z_1]^{-1} \quad \text{and} \quad A_2 = z_2[k_{12}Z_1 + Z_2]^{-1} \quad (6)$$

where  $z_1, z_2$  are the respective relative seed frequencies for species 1 and 2 and range from 0 to 1 such that the sum of both is 1.

$$z_1 = \frac{Z_1}{Z_1 + Z_2} \quad \text{and} \quad z_2 = \frac{Z_2}{Z_1 + Z_2}$$

$A_1, A_2$  are the respective areas available to species 1 and 2 and  $A_1 + A_2 = 1$  or a constant. These values of  $A_1$  and  $A_2$  are plotted on the x-axis and the values of  $O_1$  and  $O_2$  for the corresponding values of  $Z_1$  and  $Z_2$  are plotted on the y-axis. If two straight lines, one for each species, do not result, then these values of  $k_{12}, M_1$ , and  $M_2$  are adjusted in equations 5 and 6 until straight lines are derived. By such an iterative method, a single estimate of  $k_{12}$  is obtained.

Changes in competitive interaction under different conditions are often evaluated by comparing crowding coefficients estimated using this method (e.g., Friedman and Elberse 1976). However, since only a single estimate of  $k_{12}$  is obtained, differences between treatments cannot be evaluated with statistical confidence.

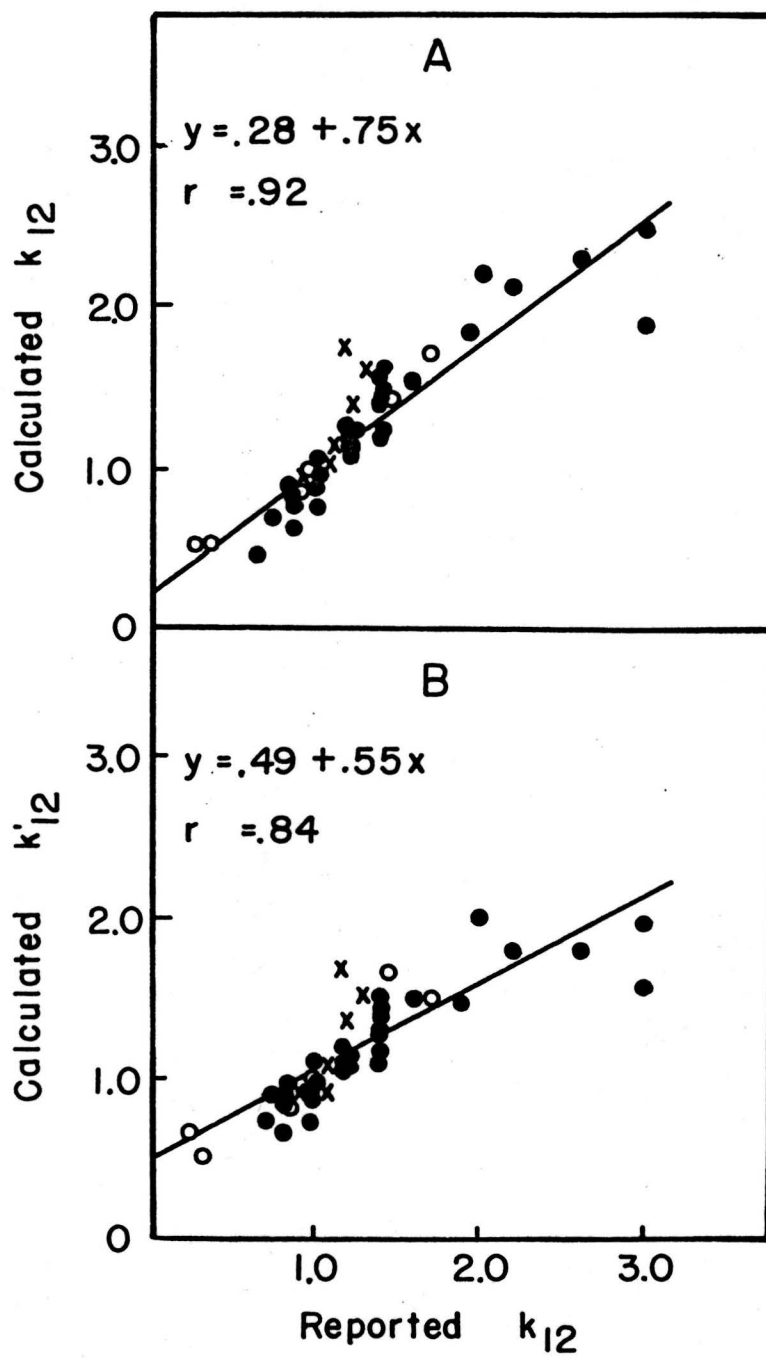
In order to treat differences of  $k_{12}$  statistically, a different method of calculation was devised. Multiple estimates of the  $k_{12}$

were derived for both the control and enhanced UV-B radiation plots by substituting values of  $O_1$  and  $O_2$  at  $Z_1 = Z_2 = 25$  seeds into equation 5. Since  $Z_1$  and  $Z_2$  were equal and thus cancel in the equation, the calculation of the  $k_{12}$  depends only on the ratio of the yields  $O_1/O_2$  for each replicate pot. The mean values of all replicate monoculture yields of species 1 and 2 were used to derive a constant value of  $M_2/M_1$ . Since an estimate of the variance of each treatment population can then be made, standard statistical tests can be performed. In this study monoculture yields (at  $z_1 = 1.0$ ,  $z_2 = 1.0$ ) were not determined. Yields under nearly monospecific stands (at  $z_1 = 0.9$ ,  $z_2 = 0.9$ ) were determined and the ratio of these yields  $M'_2/M'_1$ , was substituted for the constant  $M_2/M_1$  in equation 4. This  $k'_{12}$  was not substantially different from the  $k_{12}$  calculated by DeWit's method. Figure 4 shows the values of  $k_{12}$  reported in three different competition studies in the literature correlated with the calculated values of  $k_{12}$  and  $k'_{12}$  using the method described above. To determine  $k'_{12}$ , values of  $M'_2/M'_1$  were interpreted from the reported data.

When  $k'_{12}$  equals 1.0, neither species is considered to have a competitive advantage. If  $k'_{12}$  is greater than 1.0 species 1 has the competitive advantage whereas if  $k'_{12}$  is less than 1.0, species 2 is in the position of competitive advantage. The slope of the fitted line in Figure 4b indicates that in those cases where the reported  $k_{12}$  differed from unity, if  $k'_{12}$  differed from  $k_{12}$  it was always biased to a more conservative estimate of the competitive imbalance than  $k_{12}$  (i.e.,  $k'_{12}$  was closer to 1.0 than was  $k_{12}$ ). Therefore, calculating the  $k'_{12}$  by this method gave an accurate and reasonable







estimate of the  $k_{12}$  and if  $k'_{12}$  differed from  $k_{12}$ , it would tend to always underestimate rather than overestimate the departure of  $k_{12}$  from unity.

## RESULTS

The data for each species pairs are presented separately. For four of the species pairs the densities throughout the growing season are presented first, followed by shoot biomass determinations. The total shoot biomass of each species on a unit surface area basis is one type of biomass measurement and is referred to as "shoot biomass" throughout the text. The mean biomass of individual plant shoots is also reported and is referred to as "individual shoot weight." The height and leaf area of some species were determined and are reported subsequently for these species pairs. Finally, competitive interactions are presented in the form of replacement diagrams. In these diagrams, the relative seeding frequency of the two competitors are represented along the abscissa and yield (shoot biomass or density) on the ordinates. When the curve for a species is concave downward (e.g., Curve A in Figure 5) the yield increases rapidly as the relative sowing frequency of the competitor decreases and indicates that the species has the competitive advantage. Conversely, a species is at a competitive disadvantage if the curve is concave upward (e.g., Curve B on Figure 5) since this indicates that the yield increases only after the relative sowing frequency of the competitor decreases substantially.

Four of the species pairs did not show as great an effect due to enhanced UV-B radiation. There were some significant differences for these pairs and these are briefly reported at the end of this section.

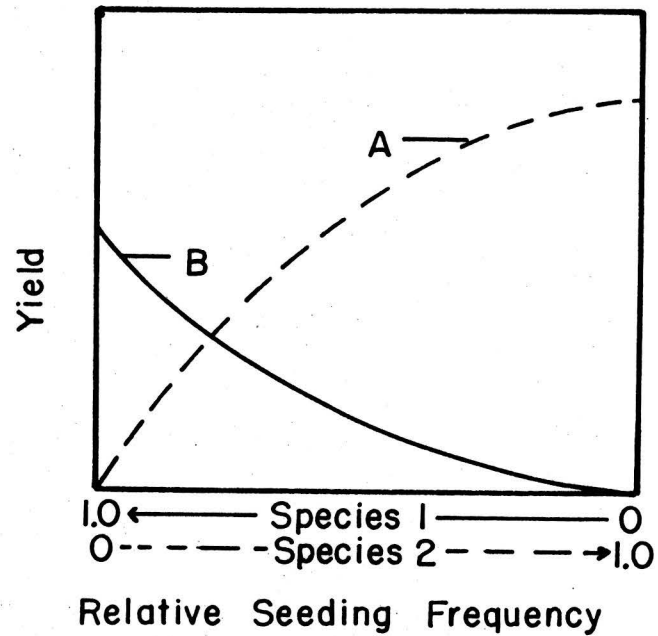


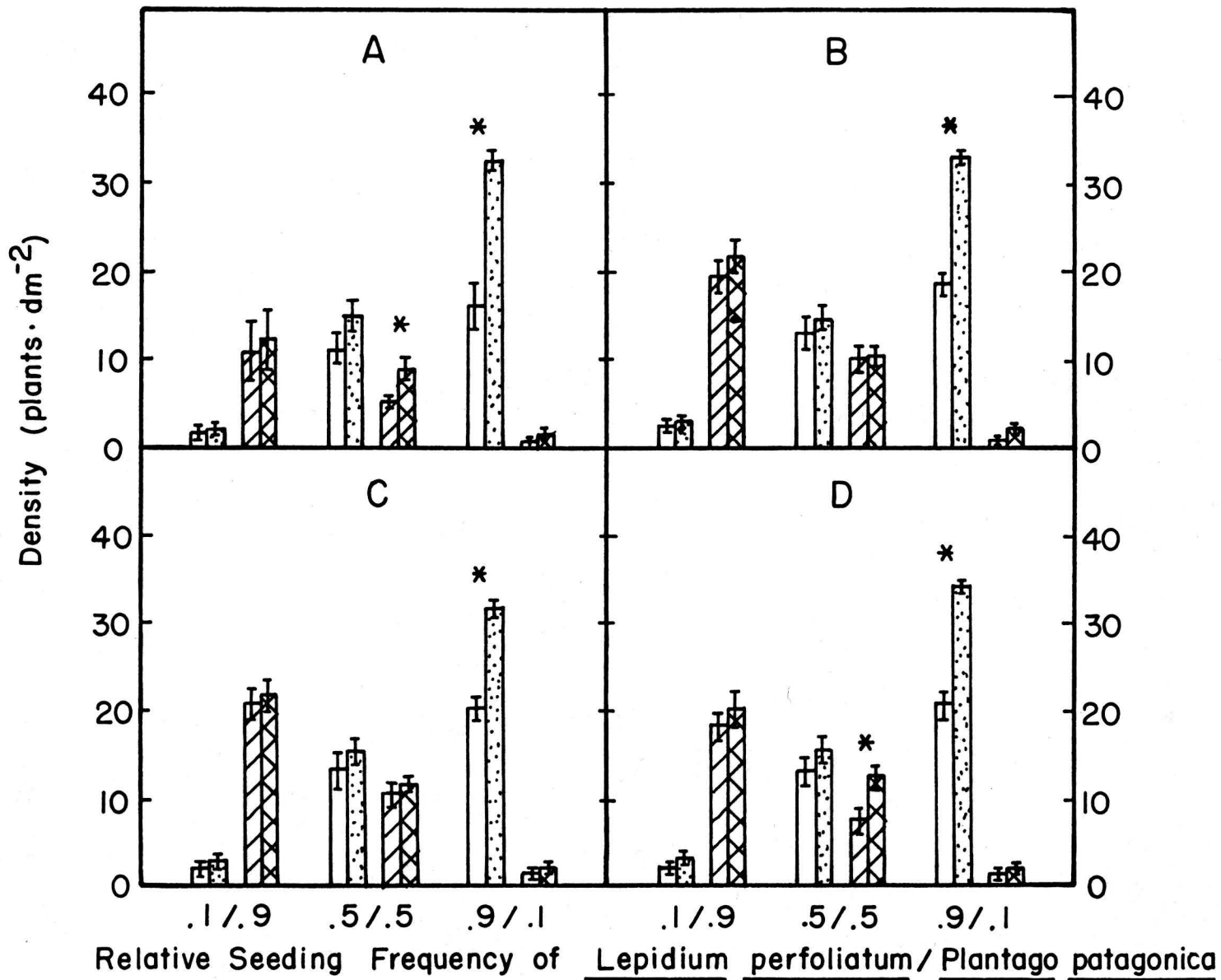
Figure 5. Replacement diagram indicating competitive interaction for a hypothetical pair of species.

Plantago patagonica: Lepidium perfoliatum

Density

The density of four sampling dates of Plantago patagonica (species 1) and Lepidium perfoliatum (species 2) are shown in Figure 6. At all sampling dates there were greater numbers of L. perfoliatum at the relative seeding frequency  $z_2 = 0.9$  when grown under enhanced UV-B radiation. The density of P. patagonica at  $z_1 = 0.5$  was higher under conditions of increased UV-B radiation at 13 and 89 days (Figure 6a and d).





### Shoot biomass

Lepidium perfoliatum ( $z_2 = 0.5$ ) had higher shoot biomass per unit area of pot surface under enhanced UV-B at the time of harvest (Figure 7a). The biomass of individual L. perfoliatum shoots at this seeding frequency was also higher while that of P. patagonica was lower as indicated in Figure 7b.

### Competitive interaction

Replacement diagrams for L. perfoliatum and P. patagonica indicating the number of surviving plants at time of harvest and the harvest shoot biomass at different relative seeding frequencies are shown in Figures 8a, b, and 8c, d, respectively. The crowding coefficients calculated from the density of surviving plants (denoted as  ${}_d k'_{12}$ ) were different for the two treatments. The  ${}_d k'_{12}$  was 0.70 for the control group and 1.30 for the enhanced UV-B treatment. However, when calculated on the basis of shoot biomass, the crowding coefficient ( ${}_b k'_{12}$ ) did not differ between the control and treatment groups.

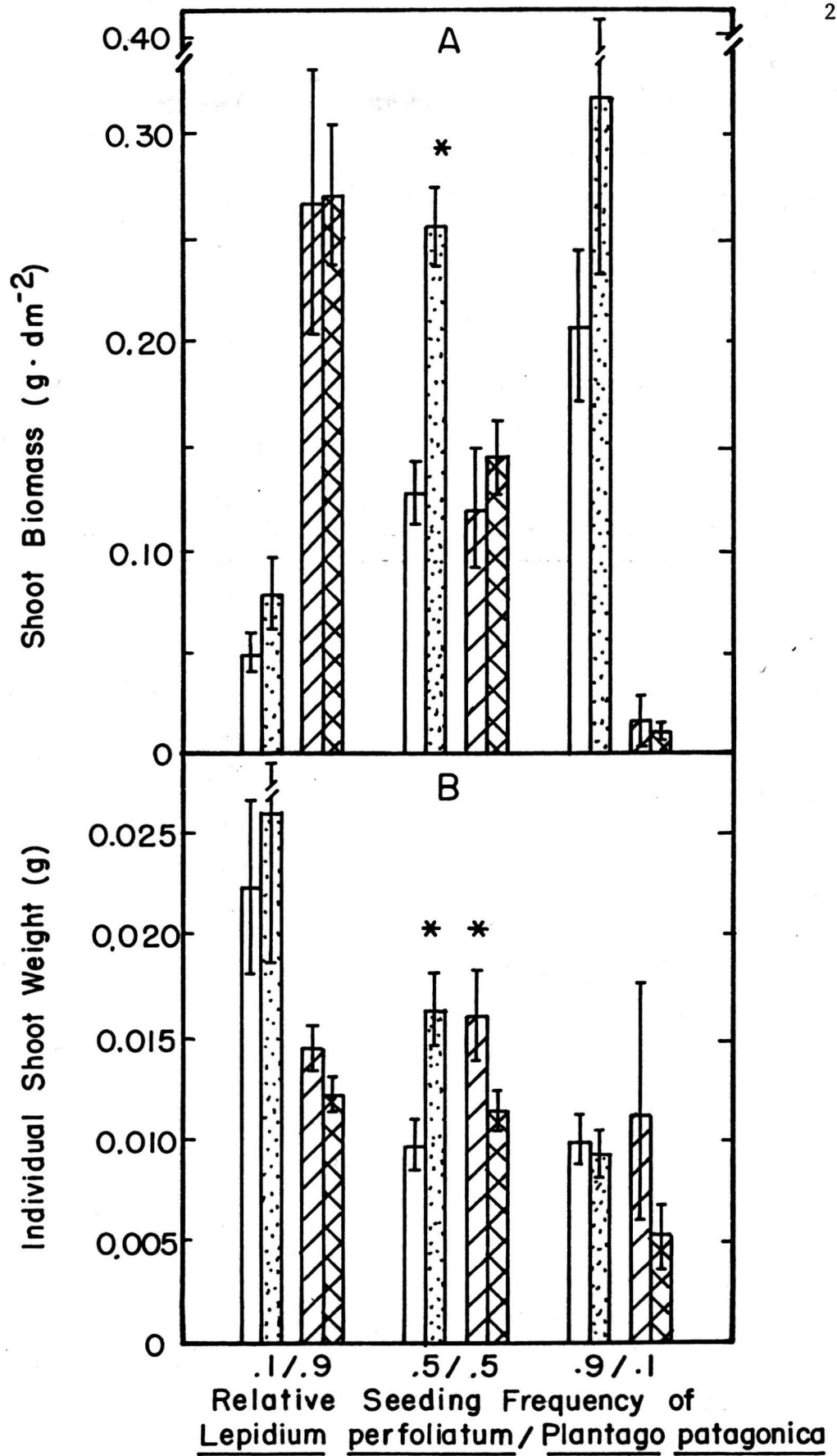
### Poa pratensis: Geum macrophyllum

#### Density

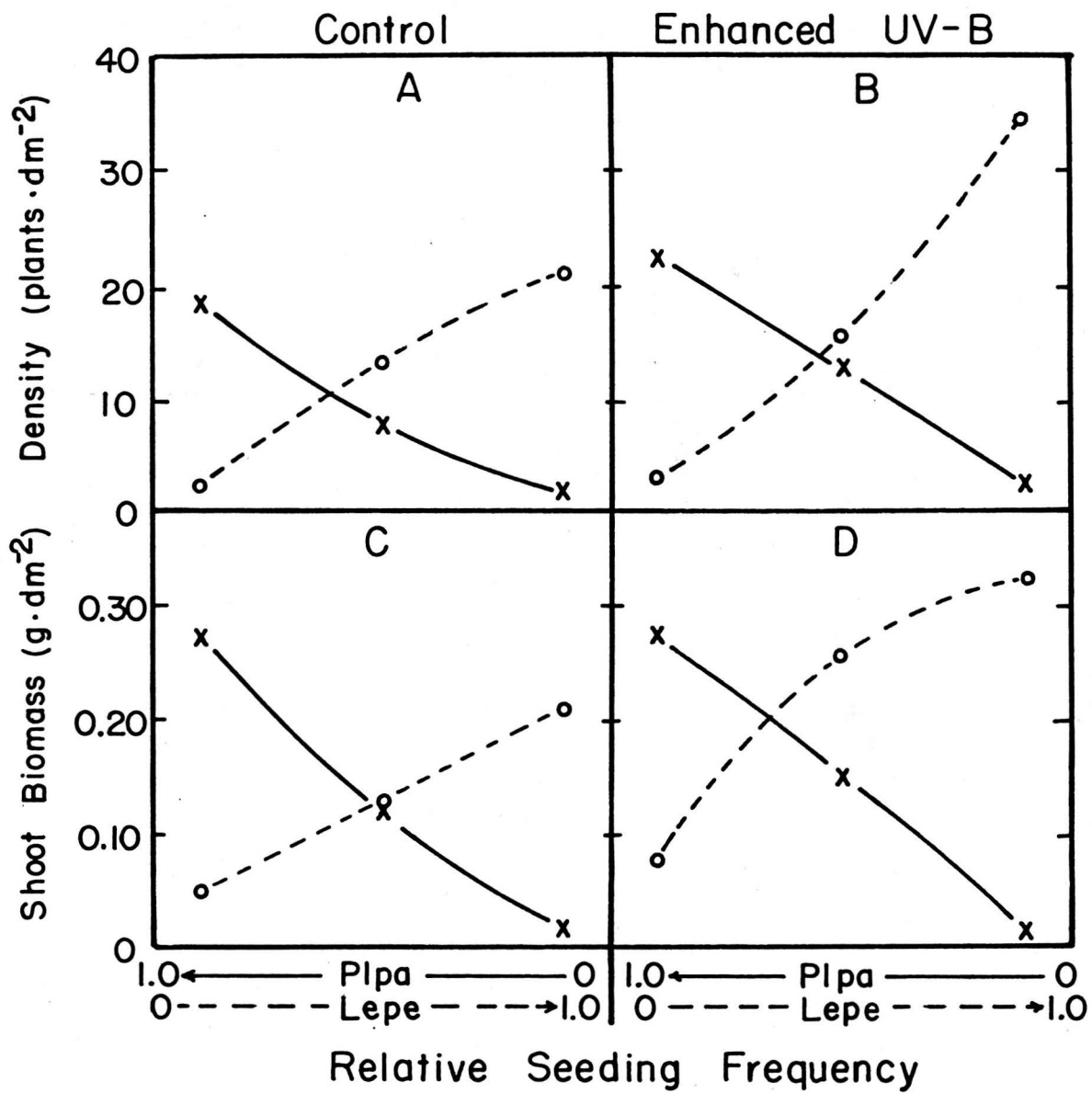
The density of Poa pratensis (species 1) at  $z_1 = 0.5$  and 0.9 was lower under enhanced UV-B radiation when sampled 13 days after sowing. At  $z_2 = 0.5$  Geum macrophyllum (species 2) exhibited lower density at the same sampling date (Figure 9a). At later sampling dates the densities of both species increased and there were no differences between treatments.



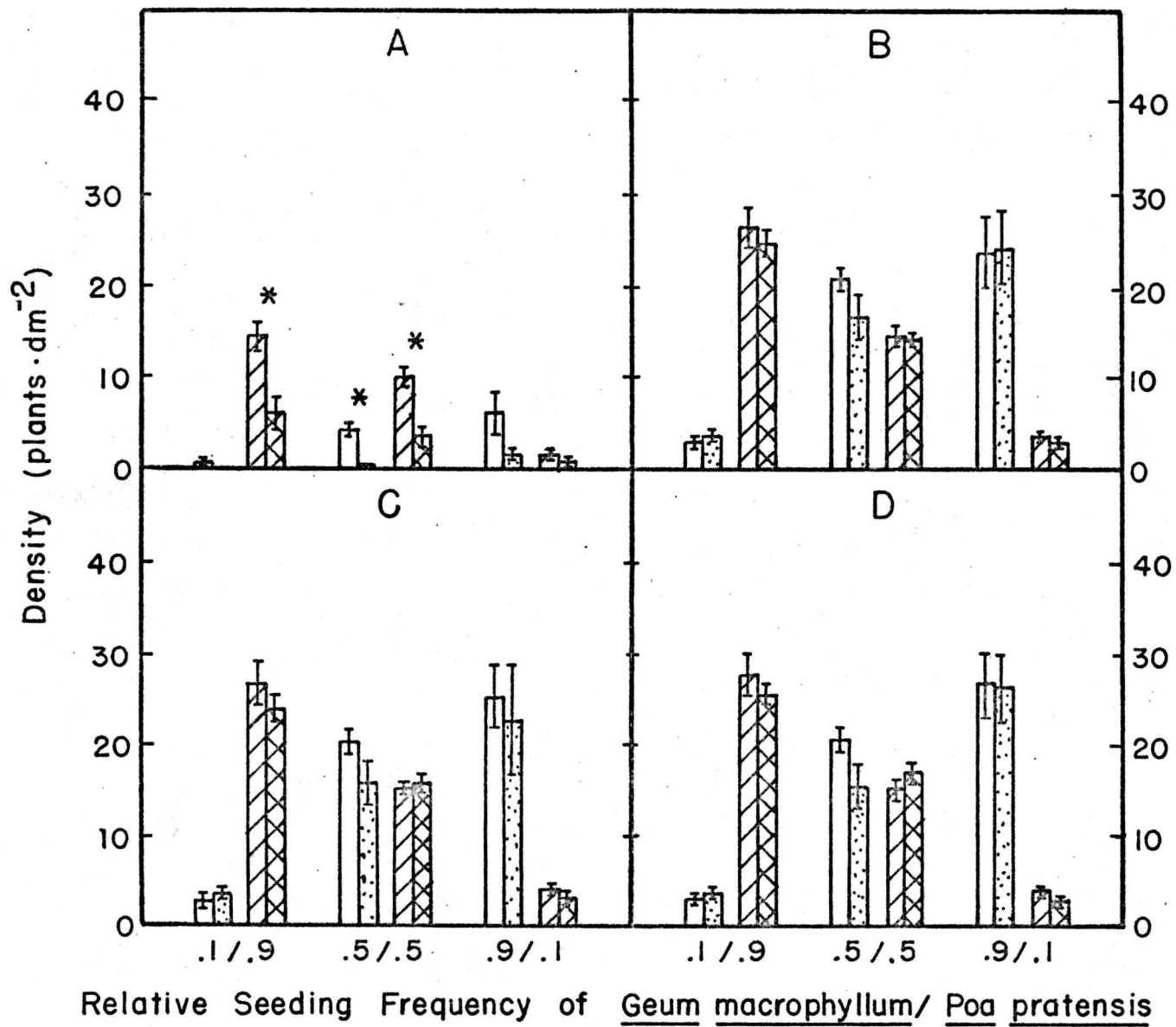












### Shoot biomass

The harvest biomass is shown in Figure 10. At  $z_1 = z_2 = 0.5$  G. macrophyllum exhibited lower shoot biomass under enhanced UV-B radiation, while P. pratensis showed an apparent increase in shoot biomass. The biomass of individual G. macrophyllum shoots at  $z_2 = 0.5$  was lower under enhanced UV-B radiation (Figure 10b).

### Competitive interaction

Replacement diagrams for P. pratensis and G. macrophyllum are shown in Figure 11. The  ${}_b k'_{12}$  values of 0.85 and 2.28 differed significantly between the control and enhanced UV-B treatments. However, the  ${}_d k'_{12}$  did not differ between treatments.

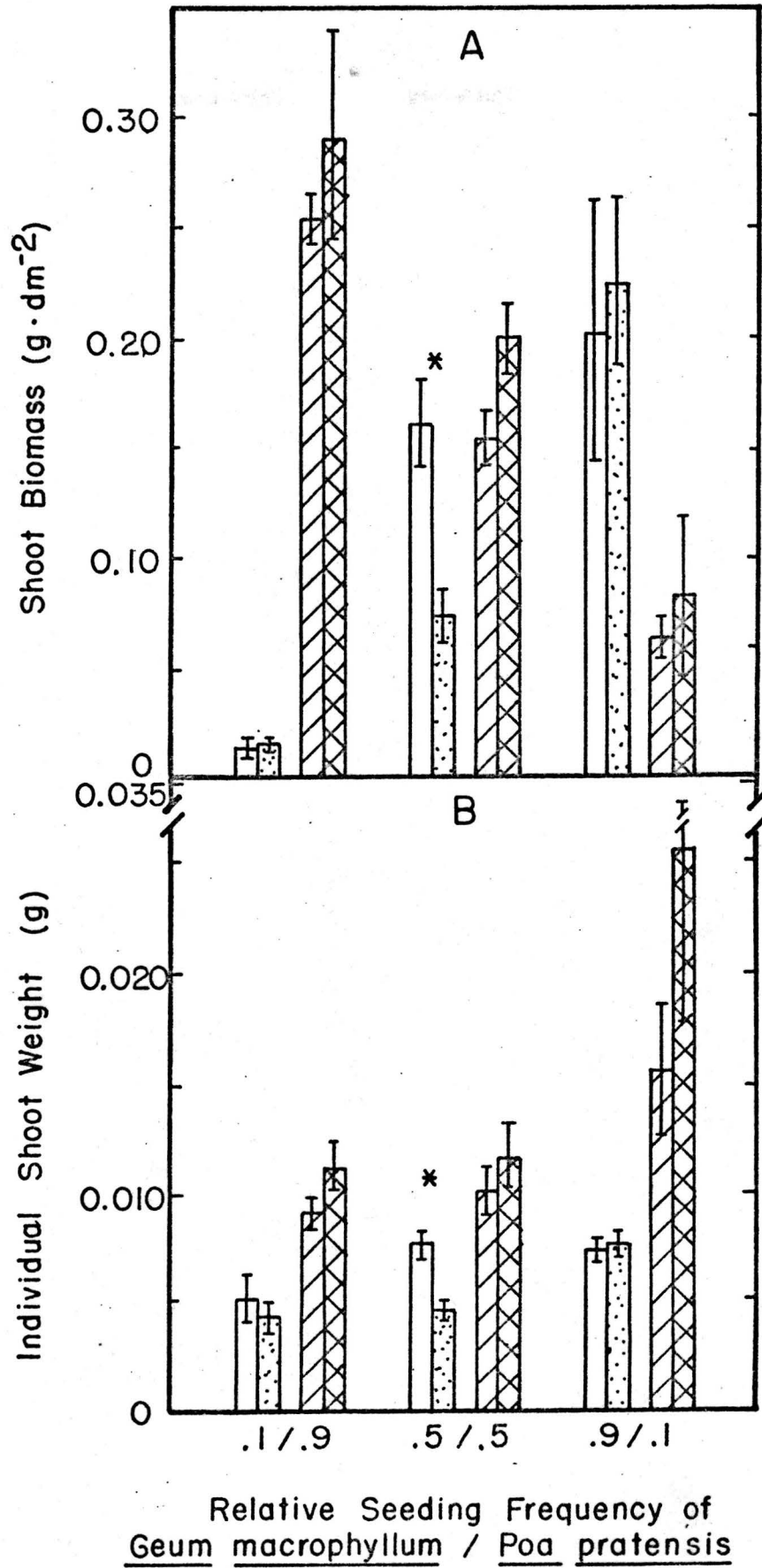
### Amaranthus retroflexus: Medicago sativa

#### Density

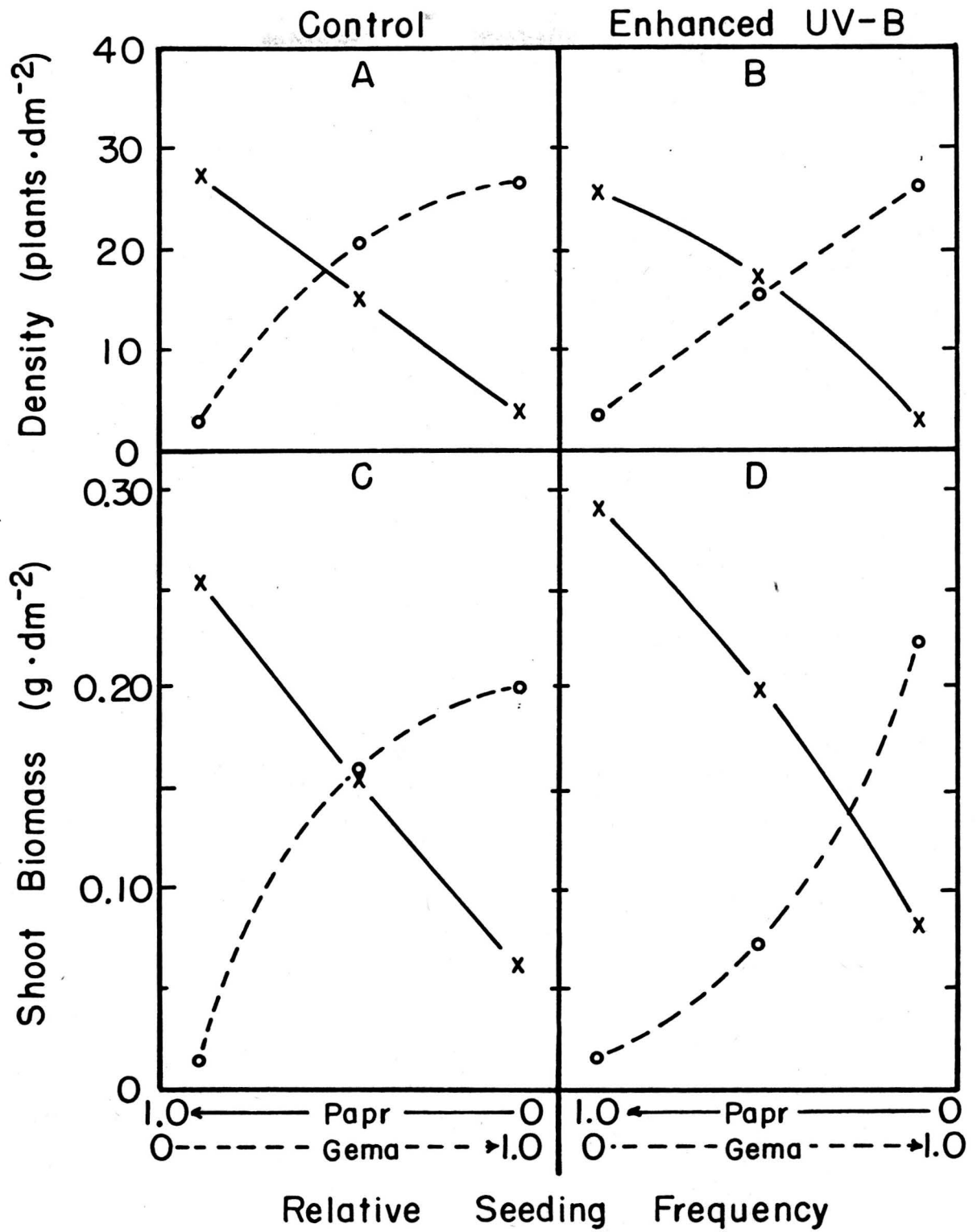
The density at four sampling dates of Amaranthus retroflexus (species 1) and Medicago sativa (species 2) grown in competition is shown in Figure 12. At 13 days after sowing, lower densities of both M. sativa and A. retroflexus occurred under the enhanced UV-B treatment when initially sown at 0.1/0.9 ratio (Figure 12a). This difference was not maintained at subsequent sampling dates, however. The density of M. sativa grown under enhanced UV-B radiation at  $z_1 = z_2 = 0.5$  increased during the season and at the time of harvest was greater than the density under the control conditions (Figure 12d).



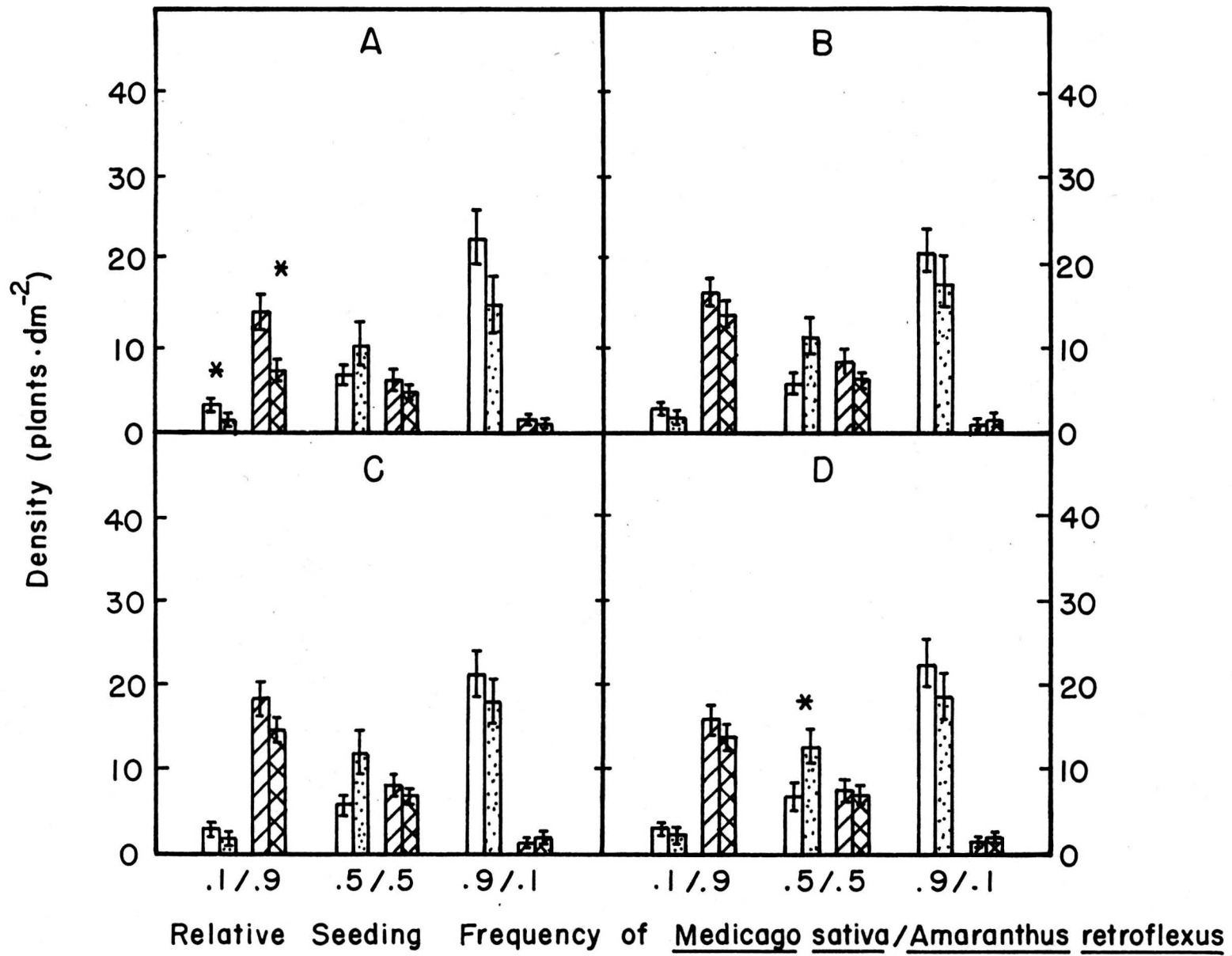












### Shoot biomass

At the time of harvest M. sativa had higher biomass per pot surface under enhanced UV-B conditions than when grown under control conditions, while A. retroflexus exhibited lower yields in enhanced UV-B conditions with respect to the controls when these species were sown at seeding frequencies  $z_1 = z_2 = 0.5$ . At higher densities ( $z_2 = 0.9$ ) the shoot biomass of M. sativa was lower when grown in the higher UV-B radiation environment (Figure 13a). The biomass of individual M. sativa shoots sown at the seeding frequency was also lower under increased UV-B radiation. Individual shoots of A. retroflexus at  $z_1 = 0.9$  and 0.5 apparently weighed less (but the difference was significant at only  $p < .10$ ) when grown at the higher UV-B radiation level (Figure 13b).

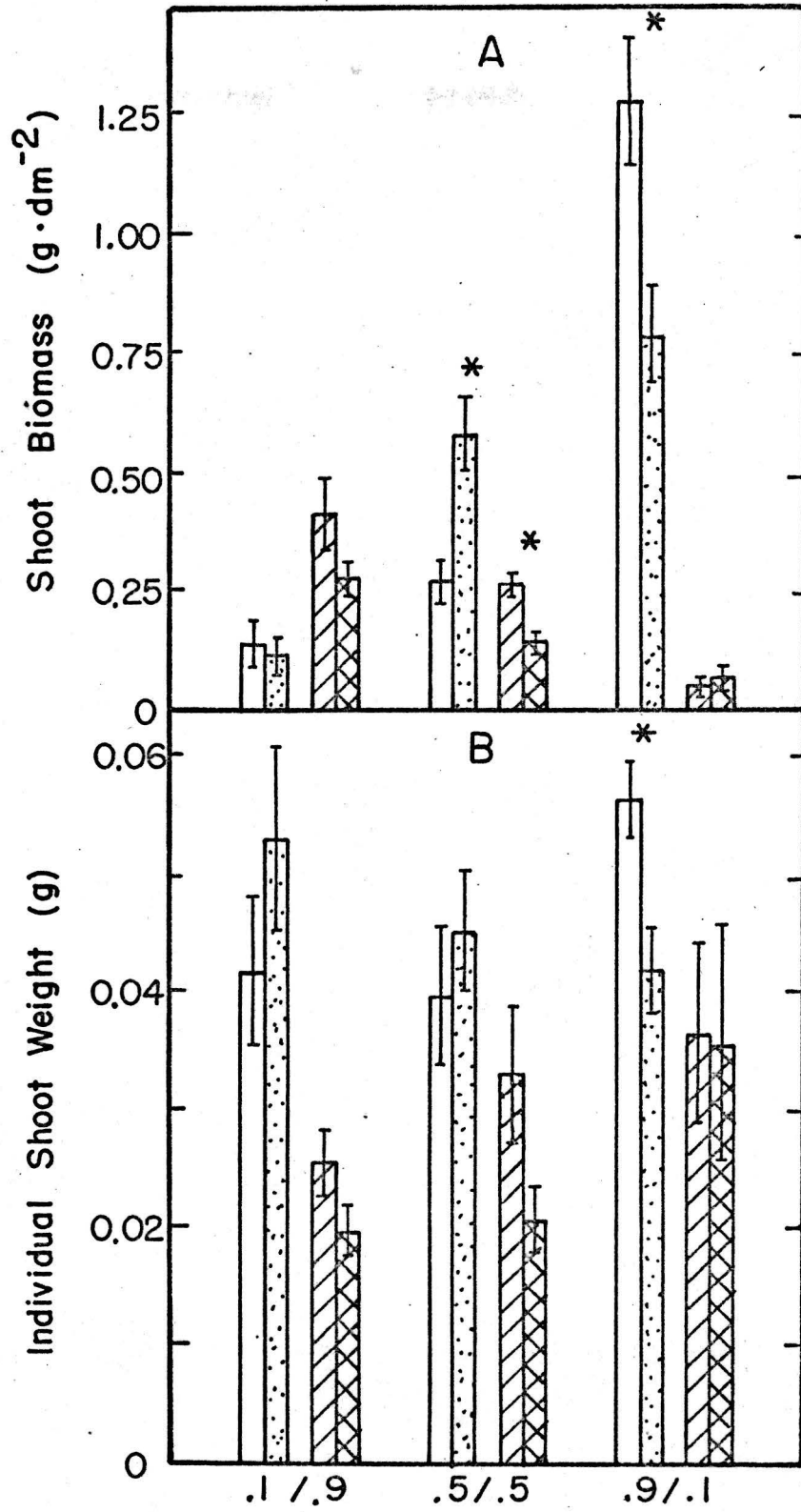
### Plant height

Plant height of A. retroflexus was reduced under increased UV-B radiation at  $z_1 = 0.9$  and 0.5 (Figure 14). The growth form of the first year M. sativa plants was a rosette and was not amenable to measurements of height.

### Competitive interaction

Replacement diagrams for M. sativa and A. retroflexus are shown in Figure 15. The  $d_{12}^{k'}$  was different for the two treatments. In the control group  $d_{12}^{k'} = 1.84$ , while  $d_{12}^{k'} = 0.71$  under conditions of enhanced UV-B radiation. The  $b_{12}^{k'}$  was 3.56 for the control conditions which differed significantly from 0.73 for the enhanced UV-B treatment.

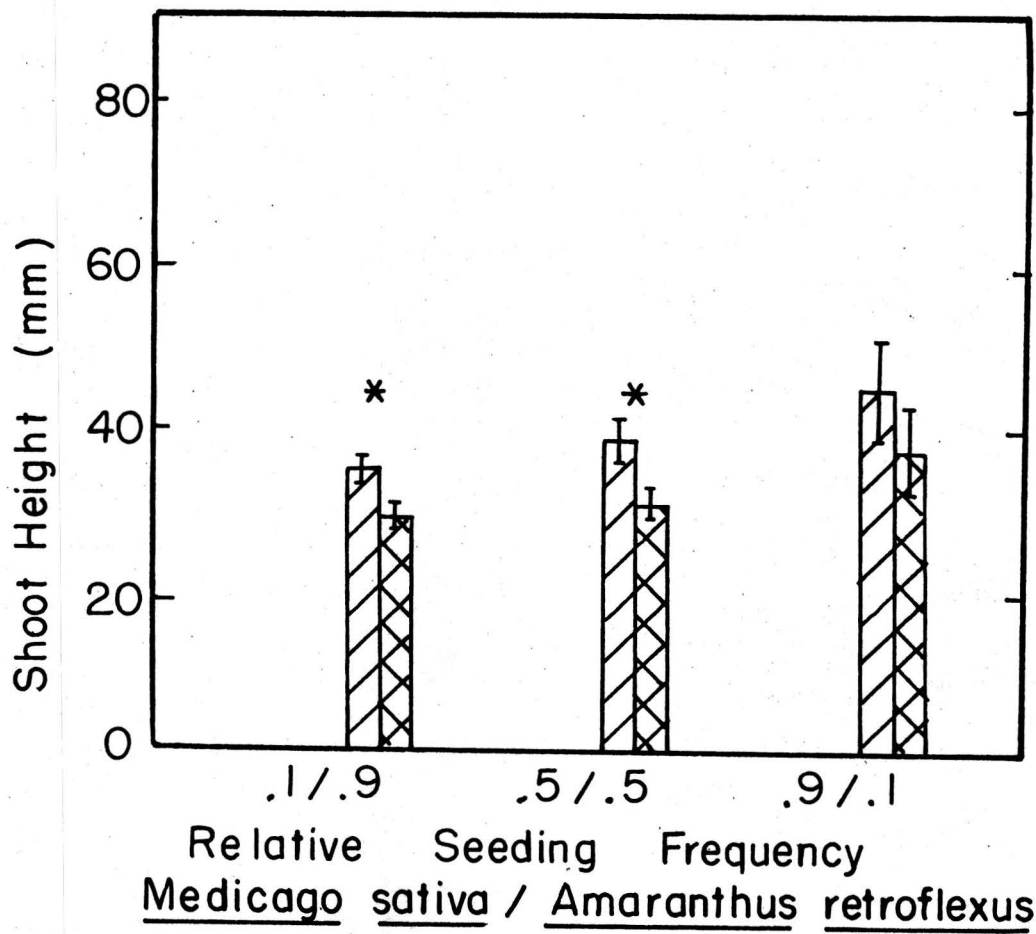




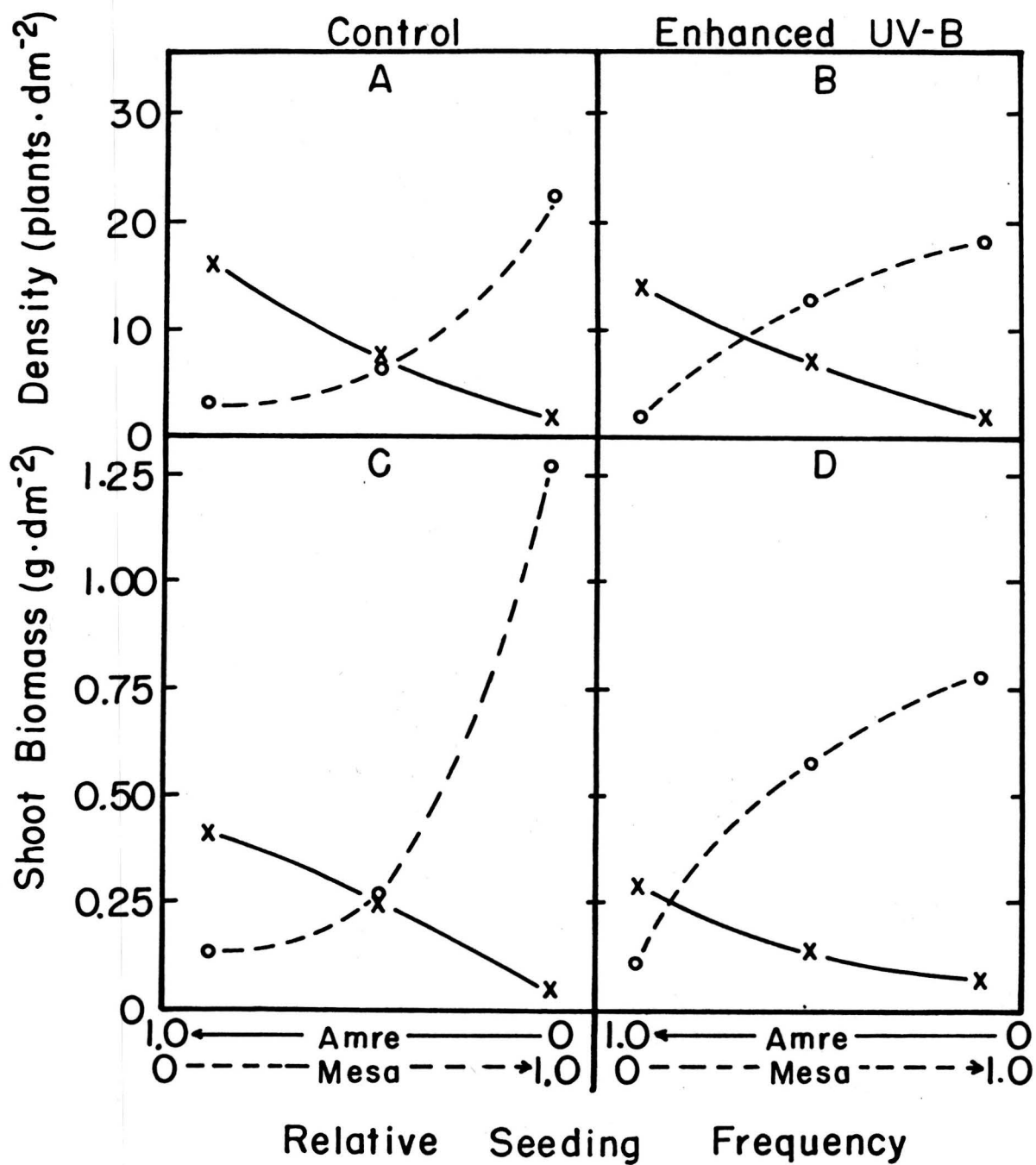
Relative Seeding Frequency of  
Medicago sativa / Amaranthus retroflexus











Alyssum alyssoides: Pisum sativum

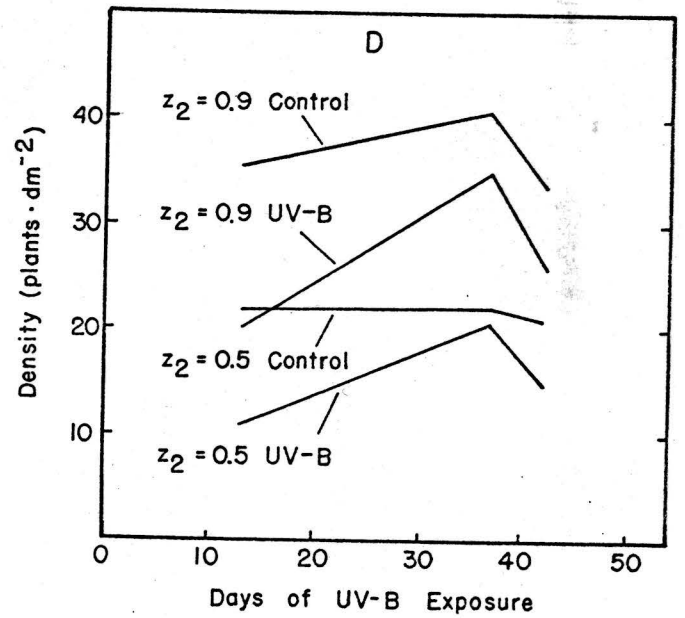
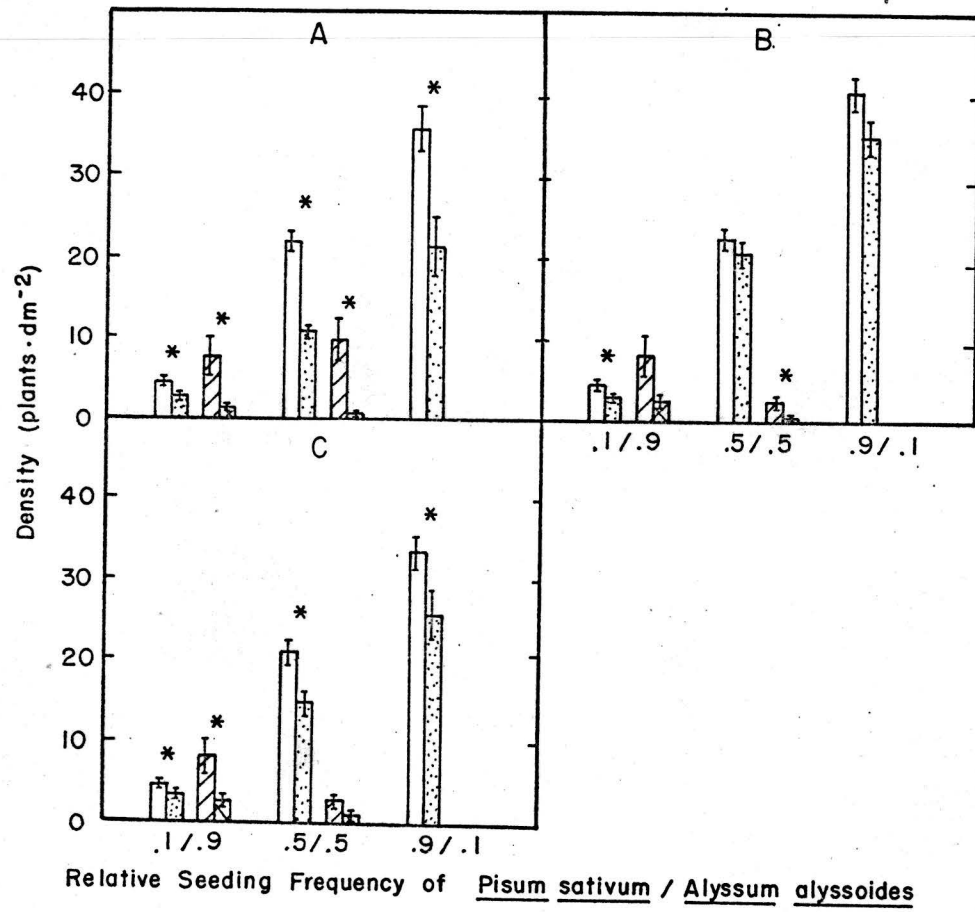
Density

Figure 16 illustrates the density of Alyssum alyssoides (species 1) and Pisum sativum (species 2) at three sampling dates after sowing. The density of A. alyssoides when sown at  $z_1 = 0.9$  was lower under conditions of enhanced UV-B radiation at 13 and 42 days after sowing (Figures 16a and c). At  $z_1 = 0.5$  A. alyssoides density was also lower at 13 and 37 days (Figures 16a and b). The number of P. sativum individuals at  $z_2 = 0.1$  was lower in the UV-B treatment group at 13, 37 and 42 days. The density of P. sativum through the growing season at  $z_2 = 0.5$  and  $0.9$  is shown in Figure 16d. The density of P. sativum increased to some extent from 13 to 37 days and then decreased by 42 days for both treatment and control groups at  $z_2 = 0.9$  and for the treatment group at  $z_2 = 0.5$ . The density of the control group at  $z_2 = 0.5$  remained constant at all sample dates. The increase and decrease in density was most pronounced for the enhanced UV-B groups at both  $z_2 = 0.5$  and  $0.9$ . The reduced density in the treatment groups was significant at 13 and 42 days but not at 37 days.

Shoot biomass

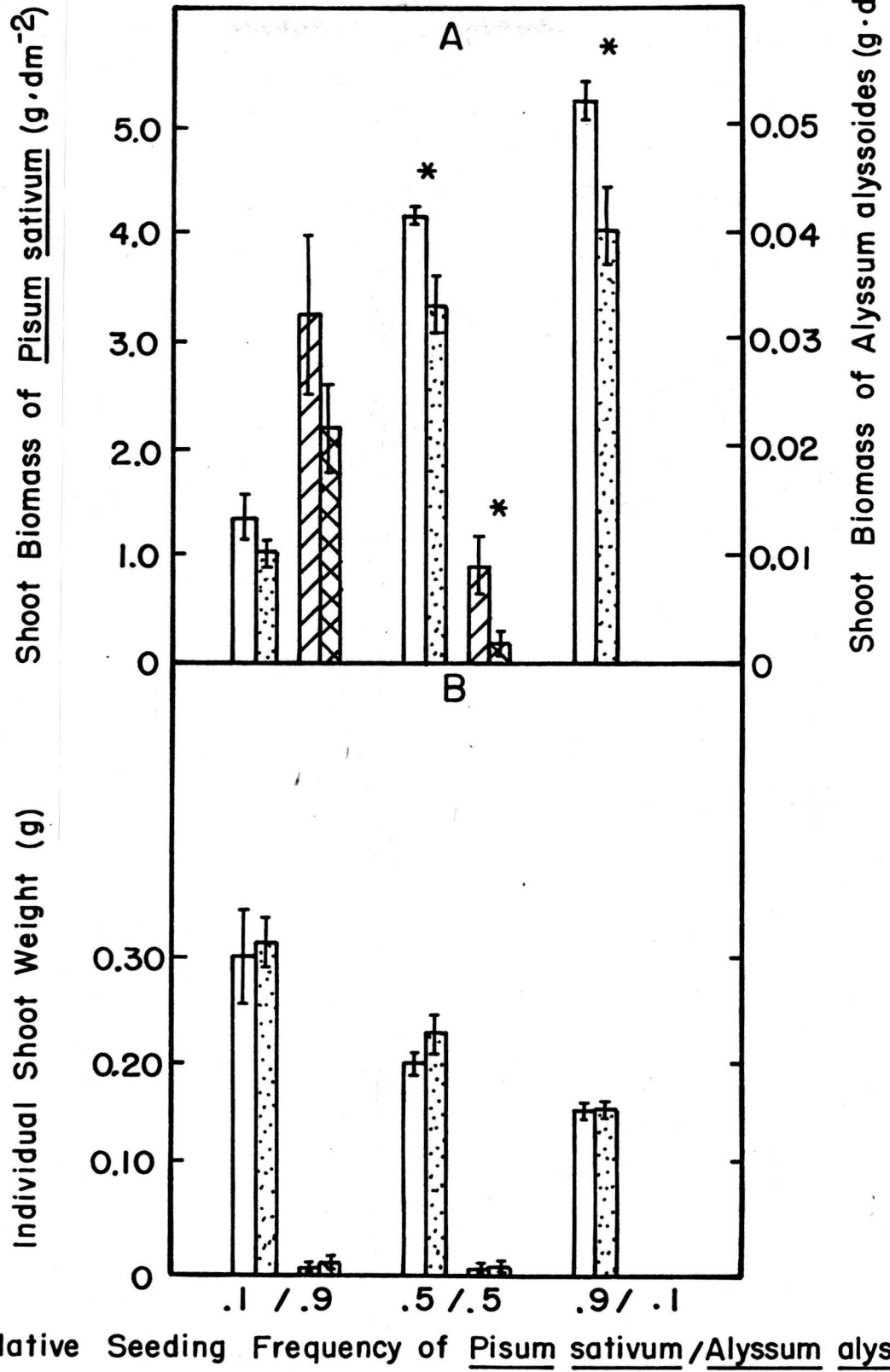
The shoot biomass of A. alyssoides at  $z_1 = 0.5$  was lower under enhanced UV-B radiation. At  $z_2 = 0.5$  and  $0.9$  the shoot biomass of P. sativum was reduced in the treatment group (Figure 17a). Neither species exhibited any differences between treatments in individual shoot weight (Figure 17b).











### Plant height

Shoot height at the time of harvest is shown in Figure 18. There was no difference in the mean height of A. alyssoides. Individuals of P. sativum grown at  $z_2 = 0.5$  and  $0.9$  were shorter in the enhanced UV-B radiation treatment.

### Leaf area of Pisum sativum

Total leaf area on an area basis at  $z_2 = 0.1$  and  $0.5$  was lower under increased UV-B radiation (Figure 19a). There was less leaf area per individual in the UV-B treatment group at  $z_2 = 0.1$ , but no difference at higher relative seeding frequencies of P. sativum (Figure 19b).

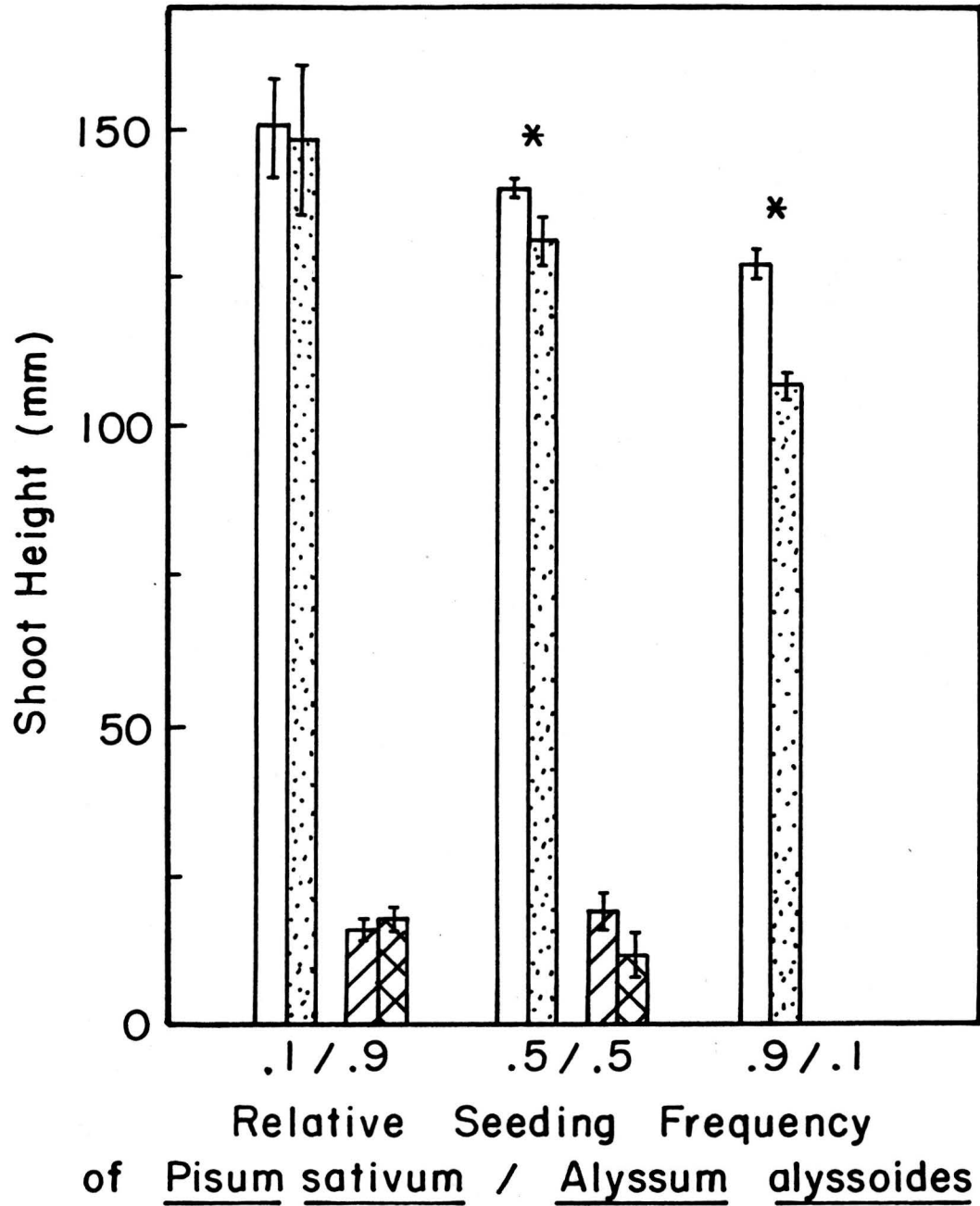
### Competitive interaction

Figure 20 illustrates replacement diagrams for A. alyssoides and P. sativum. There was no significant change in competitive interaction or outcome as indicated by the crowding coefficients. For the control and treatment groups respectively  $d_{12}^{k'}$  was 0.55 and 1.44 and  $b_{12}^{k'}$  was 0.34 and 0.25.

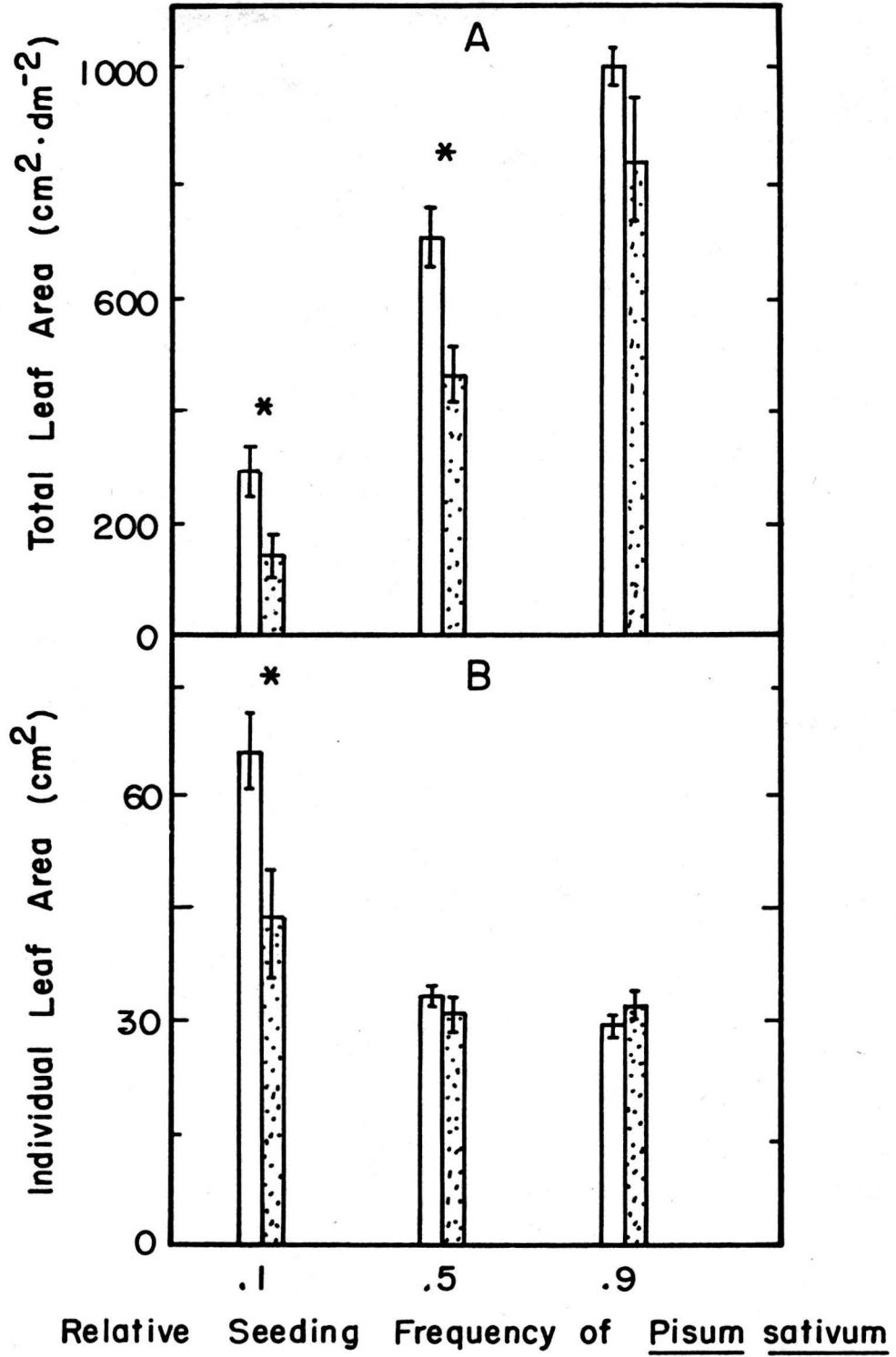
### Amaranthus retroflexus: Allium cepa

The density of Allium cepa (species 2) at 13, 50, and 70 days ( $z_1 = 0.9$ ) was higher under increased UV-B radiation, while mean shoot size measured as biomass (Table 2) and height (Figure 21) was reduced. The height of A. cepa was also reduced at  $z_1 = 0.5$  and  $0.1$ , as was the height of Amaranthus retroflexus (species 1) at  $z_2 = 0.9$ .

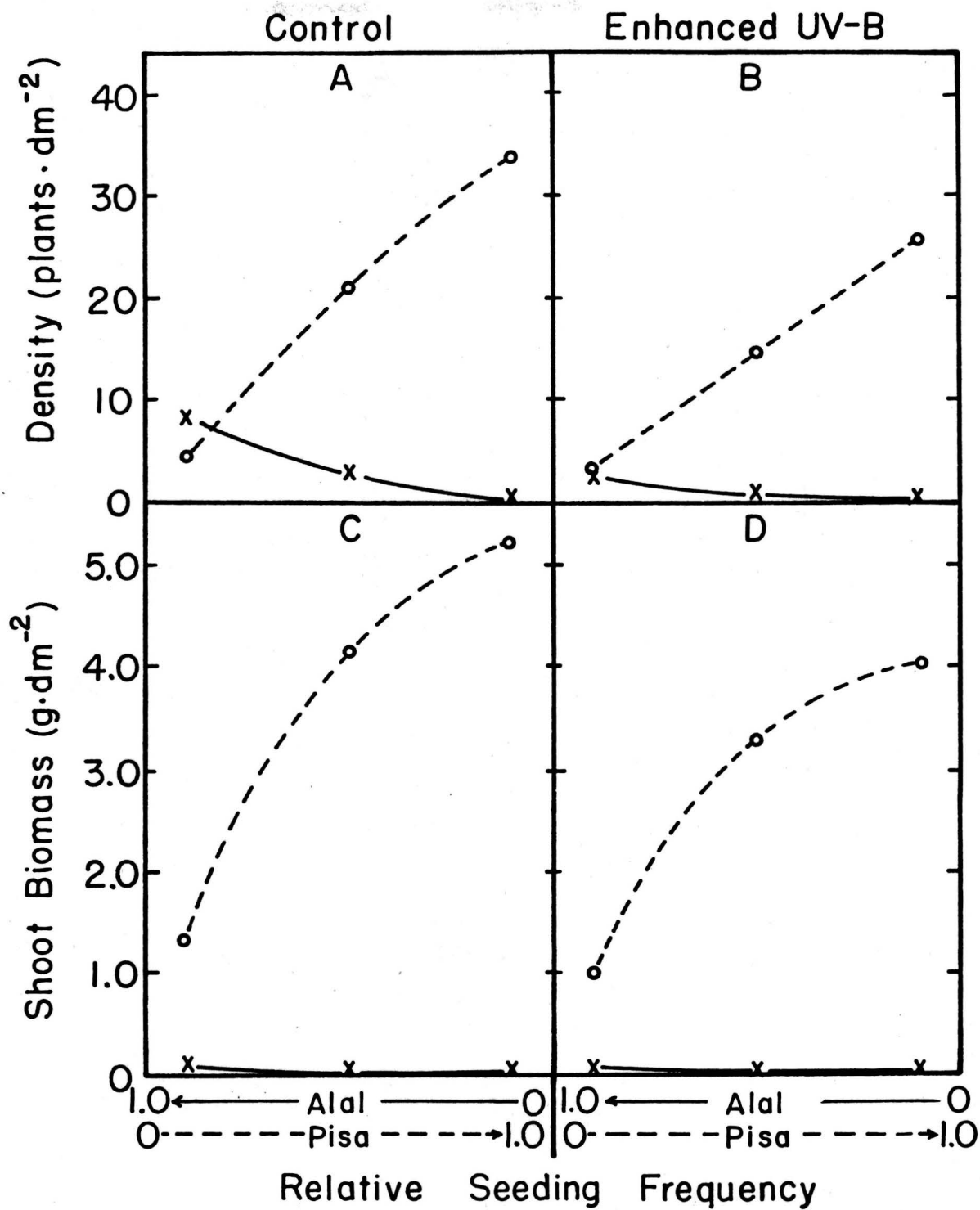






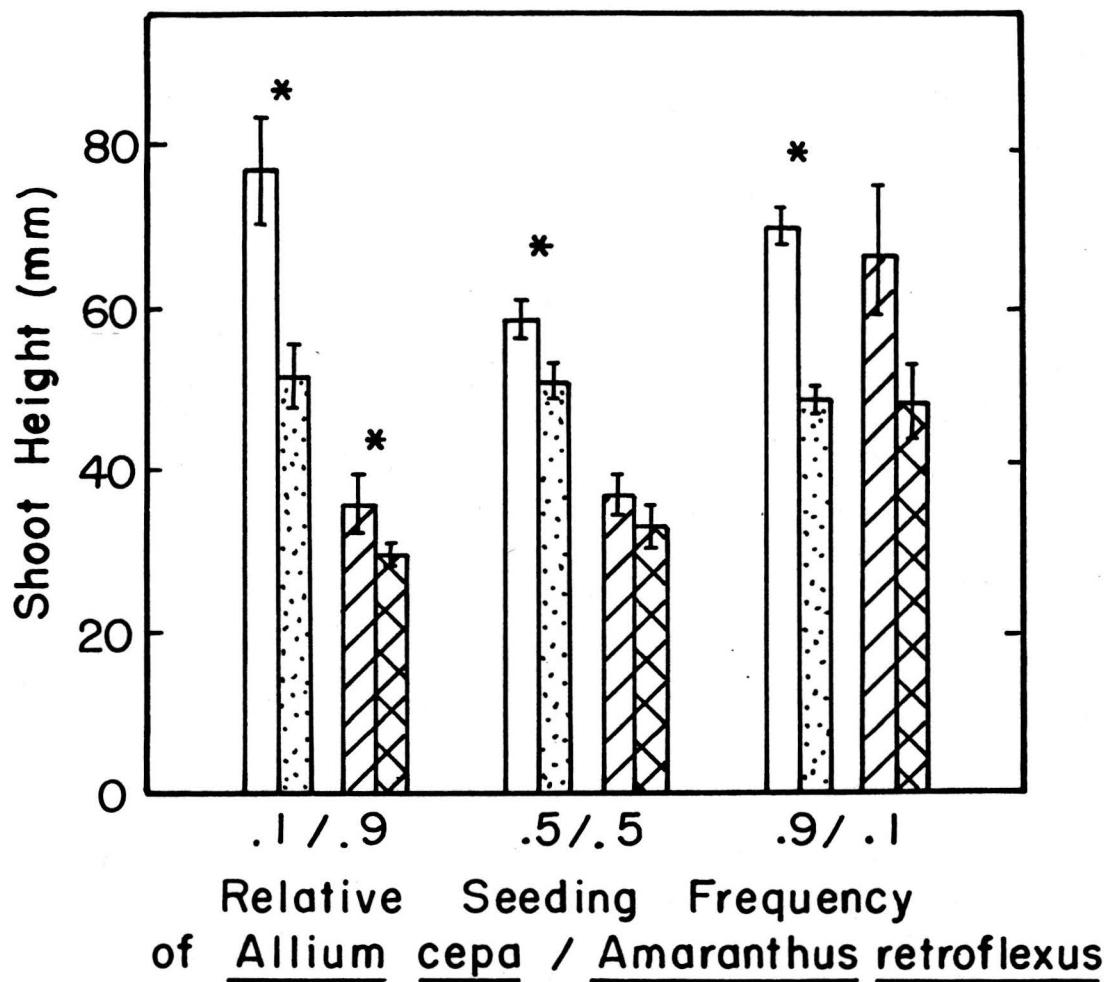












Bromus tectorum: Alyssum alyssoides

The density of Alyssum alyssoides (species 2) at 13 days was lower in the UV-B treatment at  $z_2 = 0.1$ , but was higher at 37, 50, and 89 days at  $z_2 = 0.9$  (Table 2). The density of Bromus tectorum (species 1) at 37, 50, and 89 days was lower at  $z_1 = 0.9$  for the increased UV-B treatment. At harvest the total shoot biomass and the individual shoot biomass was increased in the UV-B treatment for B. tectorum at  $z_1 = 0.9$  and A. alyssoides at  $z_2 = 0.5$  (Table 2).

Brassica nigra: Medicago sativa

Grasshoppers defoliated and killed all Brassica nigra (species 1) plants by 37 days after sowing, terminating the experiment. The only significant change noted previous to this event was reduced B. nigra density at  $z_1 = 0.5$  in the UV-B treatment group (Table 2).

Setaria glauca: Trifolium pratense

Trifolium pratense (species 2) exhibited reduced seedling density at 13 and 37 days after sowing at  $z_2 = 0.5$  under enhanced UV-B conditions. At harvest, Setaria glauca (species 1) plants sown at  $z_1 = 0.9$  weighed less when grown under the UV-B treatment (Table 2).

Table 2. Response of competing species pairs to two levels of UV-B radiation.

Competing Species Pair	Frequency	Density (plants·dm <sup>-2</sup> ) at Sampling dates								Shoot biomass (g·dm <sup>-3</sup> )		Individual plant weight (g)		Shoot height		Relative crowding coefficient						
		A		B		C		D		Con-trol	UV	Con-trol	UV	Con-trol	UV	Con-trol	UV	d <sup>k</sup> <sub>12</sub>		b <sup>k</sup> <sub>12</sub>		
		Con-trol	UV	Con-trol	UV	Con-trol	UV	Con-trol	UV									Con-trol	UV	Con-trol	UV	Con-trol
<u>Bromus tectorum</u>	z <sub>1</sub> = .1	2.8	3.2	3.8	4.4	3.8	4.2	3.8	4.2	.4639	.4459	.1221	.1062									
	z <sub>1</sub> = .5	10.2	9.8	14.4	14.0	13.2	12.6	15.6	13.6	.8825	.8087	.0566	.0595									
vs	z <sub>1</sub> = .9	21.8	18.0	32.6 *	25.8	31.0 *	21.8	34.6 *	25.2	.8063 *	1.2589	.0233 *	.0498									
	z <sub>2</sub> = .1	2.2 *	0.2	2.2	1.8	2.2	1.6	2.2	1.6	.0135	.0081	.0061	.0054									
<u>Alyssum alyssoides</u>	z <sub>2</sub> = .5	4.8	9.6	7.4	10.4	7.6	10.2	7.4	9.8	.0593 *	.1102	.0080 *	.0113									
	z <sub>2</sub> = .9	9.6	16.8	11.6 *	20.0	11.2 *	19.4	11.6 *	20.2	.1706	.2565	.0147	.0127				.92	1.19	6.35	1.63		
<u>Amaranthus retroflexus</u>	z <sub>1</sub> = .1	1.6	1.6	1.4	1.6	1.4	1.6	1.4	1.6	.2029	.0963	.1449	.0602	65.9	47.9							
	z <sub>1</sub> = .5	6.4	7.8	7.8	8.8	7.6	8.6	6.8	8.4	.2734	.2744	.0402	.0327	36.5	32.3							
vs	z <sub>1</sub> = .9	14.0	18.4	15.2	19.8	15.6	19.2	14.6	19.4	.4733	.5217	.0324	.0269	35.7 *	29.6							
	z <sub>2</sub> = .1	1.8	1.0	2.0	3.2	1.8	2.8	2.0	3.2	.0231	.0351	.0115	.0109	69.9 *	48.5							
<u>Allium cepa</u>	z <sub>2</sub> = .5	5.0	7.6	5.8	9.8	5.6	9.6	5.6	9.6	.0581	.1022	.0104	.0107	58.4 *	50.6							
	z <sub>2</sub> = .9	12.0 *	20.2	12.2	20.2	10.4 *	20.0	8.6	19.4	.1194	.2050	.0139 *	.0106	76.7 *	51.6	.74	1.08	1.89	2.01			
<u>Brassica nigra</u>	z <sub>1</sub> = .1	1.8	1.0	1.8	1.2																	
	z <sub>1</sub> = .5	14.8 *	3.6	14.6 *	4.8																	
vs	z <sub>1</sub> = .9	23.2	18.8	22.0	19.6																	
	z <sub>2</sub> = .1	17.4	11.4	16.0	10.8	17.8	11.6			.4051	.2657	.0214	.0171									
<u>Medicago sativa</u>	z <sub>2</sub> = .5	9.0	5.0	10.2	6.4	11.6	6.8			.1953	.1085	.0168	.0160									
	z <sub>2</sub> = .9	0.8	1.0	1.0	1.4	0.4 *	1.4			.0085	.0239	.0228	.0224				1.28	.60				
<u>Setaria glauca</u>	z <sub>1</sub> = .1	1.0	1.2	2.4	2.6	2.2	2.6	2.4	2.8	.2536	.3541	.1057	.1265									
	z <sub>1</sub> = .5	5.8	5.2	15.4	15.4	15.4	16.0	16.0	16.0	.8649	1.0955	.0541	.0685									
vs	z <sub>1</sub> = .9	20.6	12.2	30.4	29.3	29.4	30.0	30.2	31.4	1.4772	1.1452	.0489 *	.0365									
	z <sub>2</sub> = .1	0.4	0.2	0.4	0.2	0.4	0.2	0.4	0.2	.0114	.0087	.0286	.0437									
<u>Trifolium pratense</u>	z <sub>2</sub> = .5	3.2 *	1.0	4.0 *	1.4	3.6	1.8	3.0	1.8	.1671	.0555	.0557	.0308									
	z <sub>2</sub> = .9	5.2	7.4	7.6	8.6	7.8	8.6	8.6	8.4	.6211	.5404	.0722	.0643				2.06	2.49	2.06	18.74		

\* Significant at P<.05.

## DISCUSSION

Competitive response of populations is more clearly understood if other information on individual plant responses is also available. The relationship between population and individual plant parameters in the framework of competitive balance as influenced by UV-B irradiation will be discussed. This will be followed by an examination of the response of seedlings to enhanced UV-B irradiance. Finally the specific hypotheses posed in the Introduction will be addressed.

Amaranthus retroflexus: Medicago sativa

In the competitive mixture of A. retroflexus and M. sativa the increase in shoot biomass (Figure 13) for M. sativa at the intermediate seeding frequency ( $z_2 = 0.5$ ) was due to greater numbers of plants (Figure 12d) and was not the result of a change in mean plant weight, while the decrease in shoot biomass at higher seeding frequency ( $z_2 = 0.9$ ) was due to a decrease in the mean weight of each individual and not to a change in the number of plants. The decrease in shoot biomass at  $z_1 = 0.5$  for A. retroflexus was due to an apparent decrease in the weight of individual plants. This decrease in plant size was obscured by the presence of flower and seed heads on some of the A. retroflexus individuals which contributed to a large variance in the mean shoot weights. However, the size difference is clearly illustrated by the reduction of plant height under the enhanced UV-B conditions.

Plant response to competitive stress is not limited to fluctuations in mortality but may also include considerable change in individual plant size. Palmblad (1968) reported that Capsella bursa-pastori responded to increasing interspecific competition by maintaining a relatively high density of smaller individual plants. Increased UV-B radiation did not cause higher mortality in M. sativa grown at high density ( $z_2 = 0.9$ ) but did result in the same density of smaller individual plants when compared to the control. This apparently was also the case for A. retroflexus grown at  $z_1 = 0.9$  and 0.5. At somewhat higher levels of interspecific competition from A. retroflexus ( $z_1 = z_2 = 0.5$ ) M. sativa had higher mortality in the control group compared to the group receiving enhanced UV-B radiation, while the mean plant weight of the two groups remained the same.

The largest mean individual shoot weight of M. sativa occurred under conditions of lowest interspecific competitive stress ( $z_2 = 0.9$ ) and the lesser UV-B radiation load. In the control plants the reduction in plant weight at the other two seeding frequencies from this maximum value could only be the result of increased competition from A. retroflexus. However, in the UV-B treatment group the reduction of individual plant weight occurred under the lowest level of interspecific ( $z_2 = 0.9$ ) competition, and therefore was apparently the result of UV-B induced damage. Since growth of the M. sativa population appears to be impaired by UV-B radiation and interspecific competition did not exacerbate the depression of individual plant growth, the higher shoot biomass produced under enhanced UV-B

radiation at  $z_2 = 0.5$  is initially perplexing. There was a reciprocal adjustment in biomass between the two species in which M. sativa succeeded at the expense of A. retroflexus. This indicated that the competitive ability of M. sativa was less adversely affected by UV-B radiation than was the competitiveness of A. retroflexus. The competitiveness of Medicago under elevated UV-B radiation was clearly shown by the value of  ${}_b k'_{12} = 0.73$  (Figure 15). Since it was less than 1.0, this indicates that M. sativa had a competitive advantage over A. retroflexus. The situation under the control conditions was reversed, with Amaranthus being the more competitive species as indicated by a  ${}_b k'_{12}$  greater than 1.0 (3.56). Therefore, although both species were affected by UV-B radiation, the competitive balance shifted in favor of Medicago under enhanced UV-B radiation. The change in  ${}_d k'_{12}$  from 1.84 to 0.71 also indicated that competitive interaction had changed.

The  ${}_d k'_{12}$  is probably not as good an indicator of competitive balance as is the  ${}_b k'_{12}$ . Except for vegetatively reproducing species, the density of shoots is likely not as indicative of competitive ability as is the total biomass produced by the species. Since biomass is a reflection of the amount of resources utilized by a species, the competitive success of that species would seem to be better expressed by total biomass, rather than the number of individuals in the population. Imagine the hypothetical situation of two species, each grown in competition with a third species which maintains the same biomass and density when grown with either competitor. If the first species produces a few individuals of large

size then it would appear to be as successful against the competitor as would the second species which produced the same total biomass but from many individuals of smaller size. Thus the  $b_k'_{12}$  which is calculated from biomass measurements would seem to be the better indicator of competitive balance. However, the manner in which species interact competitively with each other may change independent of the competitive balance as indicated by total biomass. In another hypothetical situation, the biomass produced by each of two competitors might not change under two treatments, while the number and size of individuals resulting in that constant biomass might differ between the treatments. Thus, the competitive interaction would have apparently changed while competitive balance, taken as total biomass, would not. Computation of the  $d_k'_{12}$  depends on density and would thus seem to reflect competitive interaction.

Van, Garrard, and West (1976) measured photosynthesis and biomass of thirteen crop species and noted that none of the four species having the  $C_4$  pathway of carbon assimilation were susceptible to elevated UV-B irradiance. Amaranthus retroflexus, a  $C_4$  species (Welkie and Caldwell 1970) showed sensitivity to UV-B radiation in this study.

#### Plantago patagonica: Lepidium perfoliatum

At the time of harvest the increased density (Figure 6) of L. perfoliatum ( $z_2 = 0.9$ ) when grown with P. patagonica caused the apparently higher (albeit statistically insignificant) shoot biomass



(Figure 7) since the weight of individual shoots did not change. An increase in individual L. perfoliatum shoot weight, however, accounted for increased shoot biomass at  $z_2 = 0.5$ . There was no change in the shoot biomass produced by P. patagonica ( $z_1 = 0.5$ ) due to increased UV-B radiation. The constant biomass was the result of a greater number of individuals of smaller size surviving in the UV-B treatment group. The differences in density of survivors which occurred in both species are reflected in the change in  $d_{12}^k$  (Figure 8). As discussed previously the  $d_{12}^k$  may be a good indication of changes in competitive interactions but is probably not a good indicator of changes in the ultimate competitive balance. The values of  $d_{12}^k$  indicate that the competitive interactions of L. perfoliatum and P. patagonica were changed under a higher UV-B radiation environment. The competitive balance did not change, however, as shown by the values of  $b_{12}^k$  which indicated that L. perfoliatum had the advantage in both cases.

Amaranthus retroflexus: Allium cepa

Another species which showed plasticity in its response was A. cepa when grown with A. retroflexus (Table 2). At high intraspecific density the shoot biomass remained unaffected. Although the mean plant size was smaller (both height and weight) this was compensated by a greater plant density.

Poa pratensis: Geum macrophyllum

A significant shift in the competitive outcome between P. pratensis and G. macrophyllum occurred under enhanced UV-B radiation (Figure 11). The values of  ${}_b k'_{12}$  indicate that G. macrophyllum had a competitive advantage in the control group and P. pratensis had an advantage under enhanced UV-B radiation. There were no significant differences in the density of surviving plants at the time of harvest for both groups (Figure 9), which is also reflected in the lack of change of the  ${}_d k'_{12}$ . Therefore, the shift in competitive balance had to be the result of differences in individual shoot biomass. The reciprocal adjustment in the shoot biomass (Figure 10) indicated that when mutual interspecific competition was most severe ( $z_1 = z_2 = 0.5$ ) the combined effects of UV-B radiation damage and competitive stress on G. macrophyllum allowed the apparently more resistant P. pratensis to utilize a larger share of the resources. At a high density of G. macrophyllum ( $z_2 = 0.9$ ) there was no difference between treatments in shoot biomass, indicating that UV-B radiation apparently did not have a direct effect on shoot biomass nor even an indirect effect mediated through intraspecific competition. However, at  $z_1 = z_2 = 0.5$  the individual shoot weight decreased in the treatment group below the value for  $z_2 = 0.9$ , but was not less than this value in the control group. The reduction was apparently the result of increased competitive stress from P. pratensis presumably because Geum was somewhat impaired by the UV radiation. In the control group, the individual shoot weight of G. macrophyllum ( $z_2 = 0.1$ ) was reduced by increased competition from

P. pratensis such that there was no difference between the treatments. The reduction of both total shoot biomass and mean individual shoot weight in G. macrophyllum in response to increasing competitive stress of P. pratensis became apparent at a lower density of P. pratensis ( $z_1 = 0.5$ ) for plants grown under a high UV-B radiation environment than for those plants grown under the control conditions.

Alyssum alyssoides: Pisum sativum

Evaluation of the competitive status of A. alyssoides and P. sativum indicates that there was no change in interaction or balance as a consequence of increasing the UV-B radiation dose, and that P. sativum had the advantage in both experimental groups (Figure 20). These interpretations must be regarded critically, however, due to some bias included in the calculations of the relative crowding coefficients for this particular species pair. The size of individual P. sativum plants and the consequent shoot biomass was substantially larger than that of A. alyssoides. Consequently  $M'_2/M'_1$  probably overestimated  $M_2/M_1$ , and the crowding coefficients may not reflect the actual balance or change in competitive interaction.

The development of the P. sativum leaf canopy was an important factor in the response of this species to UV-B radiation. Pisum sativum formed dense canopies with leaf area indices ranging from approximately 1 at  $z_2 = 0.1$  to 10 at  $z_2 = 0.9$  at the time of harvest (Figure 19). In the control groups P. sativum density was close to the maximum value even at the earliest sampling date (Figure 16d) and did not decrease until leaf canopies were well developed at which

time thinning occurred probably due to increased intraspecific competition. In the treatment group the density of plants was considerably lower at the first sampling date ( $z_2 = 0.5$  and  $0.9$ ). As the leaf area increased, the number of plants also increased. Leaves are essentially opaque to UV-B radiation. Thus a well developed canopy probably afforded some protection for developing seedlings against the UV-B radiation. The result was that no significant difference in density existed between the two groups by 37 days. Since, at this time, the number of surviving plants in the enhanced UV-B group represented most of the seeds sown (35 plants from 45 seeds for  $z_2 = 0.9$  and 20 plants from 25 seeds for  $z_2 = 0.5$ ) the large differences observed earlier could not have been the result of seedling mortality. Inhibited germination or arrested seedling emergence appear to be the cause of this difference early in the experiment. The inhibition was removed and development continued when the leaf canopy increased reducing the amount of UV-B radiation reaching the soil surface. It was also observed that the vigorous germination of P. sativum disrupted the soil surface causing seed coats to become exposed to UV-B radiation.

Enhanced UV-B radiation reduced the density of A. alyssoides and P. sativum for several seeding frequencies on many sampling dates (Figure 16). This indicated that both species were damaged by exposure to UV-B radiation. Total leaf area and shoot biomass, like density, are characteristics of populations and not of individuals, and were reduced in many instances under the increased UV-B radiation environment. With the exception of individual leaf area at  $z_2 = 0.1$ ,

neither the weight nor the leaf area of individual plants were affected. The differences in total shoot biomass at the population level between treatments were the result of differences in density. Although leaf area and weight of individual plants were not affected, shoot height of P. sativum was sensitive to elevated UV-B radiation at higher intraspecific densities (Figure 18).

Pisum sativum plants had the highest individual leaf area under conditions of lower UV-B radiation and lowest intraspecific density ( $z_2 = 0.1$ ). As the seeding frequency in the control group increased ( $z_2 = 0.5$ ) mean leaf area decreased from the higher value at  $z_2 = 0.1$  and remained at this low value as the density increased still higher ( $z_2 = 0.9$ ). In the UV-B treatment leaf area was depressed to approximately this same low level even at the lowest relative seeding frequency at  $z_2 = 0.1$ . Thus, for Pisum plants grown in control conditions, leaf area was apparently reduced as intraspecific competitive stress increased. However, the leaf area of plants raised under enhanced UV-B was low at low levels of intraspecific competition. This may have occurred because either leaf area was affected at lower levels of intraspecific competition when plants were grown under higher UV-B irradiance than when grown under lower UV-B irradiance, or because leaf area was affected directly by UV-B radiation regardless of intraspecific stress.

### Effect of Enhanced UV-B Irradiance on Seedlings

In addition to P. sativum which exhibited sensitivity to UV-B radiation at germination or seedling emergence, several other species appeared to be sensitive at the seedling stage. Lower densities were often observed at early sampling dates, but the differential disappeared by later dates (Figures 9, 12, and Table 2). This would have been due to other plants replacing those that suffered mortality as seedlings or to the renewed germination which was previously arrested. Species which exhibited the phenomenon included P. pratensis, G. marcophyllum, T. pratense, both A. retroflexus and M. sativa when grown together, and A. alyssoides, when grown competitively with B. tectorum. Density was the only parameter measured for seedlings.

Although the seedling stage appears to be a time in phenological development when several species are sensitive to UV-B radiation, how they are affected is unclear. Studies which follow individuals of the population through frequent censuses and furnish information on individual plant parameters such as seedling height and biomass would do much to elucidate the effect. Seedling mortality of plants in natural systems might be expected to be more severely influenced by UV-B radiation since water stress and competition from other species generally would be greater than in systems of well watered pot-grown plants. Plant species which germinate in June when the solar altitude is high would be exposed to greater UV-B radiation loads and usually also greater water stress than species which germinate earlier in the spring.

The concept that other stress factors may influence the expression of growth impairment by UV-B radiation has significance in the understanding of the impact of enhanced UV-B irradiance on natural systems. Specifically, the hypothesis that growth is more impaired by UV-B radiation under the most severe interspecific competition was examined in this study. The relative seeding frequency where the densities of the competitors are equivalent ( $z_1 = z_2 = 0.5$ ) should exhibit the greatest effect on growth. The hypothesis was supported in the case of Plantago patagonica, Geum macrophyllum, Trifolium pratense and Brassica nigra (Figures 6, 7, 9, 10, Table 2). The growth of these species was affected only at  $z_1 = z_2 = 0.5$ . Three other species, Bromus tectorum, Setaria glauca, and Amaranthus retroflexus when sown with Allium cepa showed effects on growth only at  $z_1 = 0.9$  (Figure 21, Table 2). These results do not support the hypothesis. This suggests that for these species, intraspecific competitive stress apparently exacerbates UV-B radiation insult more than does interspecific competition. To test the impact of intraspecific competition stress, these species would have to be grown at various densities in monoculture. Pisum sativum appeared very sensitive to UV-B irradiance and exhibited impairment of growth regardless of the degree of interspecific competition. The remaining species were apparently affected by both types of competitive stress and exhibited changes in growth at intermediate and high relative seeding frequencies in most cases.

In addition to the influences of competitive presence on the expression of UV-B damage, competitive balance itself may be affected

by increased UV-B irradiance. Competitive balance was altered in three of the species pairs studied which supports this hypothesis. The competitive interactions of Plantago patagonica and Lepidium perfoliatum changed in response to supplemented UV-B irradiance, although Lepidium maintained the competitive advantage under both UV-B irradiance treatments (Figure 8). Amaranthus retroflexus and Medicago sativa responded to UV-B irradiation by changing both competitive interaction and balance. Amaranthus was more competitive in the control group and Medicago was the better competitor in the enhanced UV-B treatment group (Figure 15). Under the control conditions Geum macrophyllum had the competitive advantage over Poa pratensis but the competitive balance was reversed under the elevated UV-B radiation conditions (Figure 11). No alteration in competitive balance were observed for the remaining species pairs.

The hypothesis that UV-B radiation influences plant growth parameters was tested. There is much evidence to support this hypothesis. Leaf area of individual plants was reduced for Pisum sativum under an enhanced UV-B radiation regime (Figure 9). Shoot height decreased for Amaranthus retroflexus, Allium cepa and Pisum sativum (Figures 14, 18 and 21). Individual shoot weight was affected for Setaria glauca, Allium cepa, Alyssum alyssoides, Bromus tectorum, Lepidium perfoliatum, Plantago patagonica, Geum macrophyllum, and Medicago sativa at various relative seeding frequencies (Figures 7, 10, and 13, Table 2). Mortality of individuals was affected and consequently at the population level the density at different sampling dates for various relative seeding



frequencies was altered for Bromus tectorum, Alyssum alyssoides, Allium cepa, Brassica nigra, Trifolium pratense, Plantago patagonica, Lepidium perfoliatum, Poa pratensis, Geum macrophyllum, Amaranthus retroflexus, Medicago sativa, and Pisum sativum (Figures 6, 9, 12, and 16, Table 2).

The final hypothesis tested in this study was that since the effect of UV-B radiation is considered to be generally detrimental to plants, when growth of a species does appear to be enhanced, then this occurs only as a result of UV radiation damage to the competing species. For the species pairs A. retroflexus vs. A. cepa, B. nigra vs. M. sativa, A. alyssoides vs. P. sativum, and S. glauca vs. T. pratense the changes which did occur in response to UV-B irradiance were always detrimental to growth (Figures 16, 17, 18, 19, and 21, Table 2). Poa pratensis when grown with Geum macrophyllum and Medicago sativa when grown with Amaranthus retroflexus showed increased growth under UV-B radiation, but there were concomitant decreases in the growth of their competitors. This change in competitive balance was also reflected in the change in  $b_{12}^{k'}$  for each pair, and thus supports the hypothesis (Figures 10, 11, 13 and 15). Bromus tectorum when grown with Alyssum alyssoides and Lepidium perfoliatum when grown with Plantago patagonica exhibited increased shoot biomass at a single seeding frequency, while their competitors exhibited no decrease (Figures 7 and 8, Table 2). However, there were no changes in competitive balance (as indicated by  $b_{12}^{k'}$ ), as one would expect as a result of an increase in shoot biomass in one species of a competing pair. There is at least

one other reason why an increase in shoot biomass of a single species might occur. If a pathogen which restricted plant growth of one species was sensitive to UV-B radiation then increased irradiance would increase the production of the plant species by reducing the effectiveness of the pathogen.

## CONCLUSIONS

This study evaluated the effects of a moderate level of supplemented UV-B irradiance on the response of plants grown in competitive situations under field conditions. The results of the study suggest the following generalizations.

1. Moderate increases in UV-B irradiance may result in changes in plant growth under field conditions.
2. The competitive balance between some plant species may shift under elevated UV-B irradiation. The apparent reason for the changes in competition is the differential sensitivity of the competitors to UV-B radiation.
3. The effect of UV-B radiation on some species may be exacerbated by interspecific competition. However, for some species, there may be a greater influence from intraspecific competitive stress.
4. Beneficial effects of UV-B radiation on plant growth probably do not occur. Species which might exhibit apparent enhanced growth with enhanced UV-B irradiation are apparently benefited as a result of shifts in competitive balance. Alternately, an enhancement could be due to suppression of plant pathogens by UV-B radiation.
5. The effect of enhanced UV-B radiation on natural or agricultural systems is difficult to determine and any predications must be evaluated cautiously and critically.

Nonetheless, I feel that this study indicates that some changes in community structure and composition as well as decreases in productivity in some agricultural systems might occur if global UV-B radiation were to increase as a result of a moderate reduction in stratospheric ozone concentration.

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