# Response of Soybean Bulk Leaf Water Relations to Ultraviolet-B Irradiation

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## Summary

Erosion of the stratospheric ozone layer by anthropogenic emission of halogenated compounds may lead to increased UV-B radiation at ground level. In 1990 soybeans (*Glycine max* (L.) Merr. cv. Essex) were grown in open-top field chambers with 3 levels of UV-B replicated 3 times. UV-B treatments corresponded to changes in the total column ozone thickness of +15 % (low), −20 % (medium) and −35 % (high). Leaves were sampled during four intervals of the growing season and subjected to pressure-volume (P-V) analysis to determine symplastic volume ($V_o$), maximum turgor pressure ($pMAX$), symplastic solute content ($N_s$), tissue elasticity coefficient ($z$), and the potential at turgor loss (TLP). Leaf conductance, average specific leaf weight (SLW), and area per leaf were measured several times during the season. During the second sampling period at 58 days after planting (DAP), $V_o$ was significantly decreased at the highest UV-B level but was not affected by UV-B treatments again. Also during the second sampling period the elasticity coefficient, $z$, in the medium and high UV-B treatments was significantly less than in the low UV-B treatment. In the fourth sampling period (100 DAP), $z$ again was significantly affected by UV-B treatment; in this case, however, while $z$ was lower in the high than the medium UV-B treatment, it did not differ from the low UV-B treatment. The relative symplastic volume at the turgor loss potential ($RSV_{TLP}$) was the only other parameter to show a significant UV-B effect, but only at the highest treatment level and only near the end of the season. Generally, the significant changes in all P-V parameters with plant age were much larger than any treatment effects. There were no significant differences in leaf conductance, leaf area or SLW, indicating that, although the leaf P-V relationships were noticeably altered, these sporadic treatment effects had little real influence on leaf water balance.

*Key words: Glycine max (L.) Merr., Conductance, Elasticity, Leaf ontology, Pressure-Volume Analysis, Soybean, Ultraviolet-B, Leaf Water Relations.*

*Abbreviations:* DAP = days after planting; $N_s$ = symplastic solute content; $P_{MAX}$ = turgor potential at full hydration; P-V = pressure-volume; R-B = Robertson-Berger; $RSV_{TLP}$ = relative symplastic volume at the turgor loss potential; SLW = specific leaf weight; TLP = water potential at turgor loss (incipient plasmolysis); UV-B = ultraviolet-B; $UV$-$B_{BE}$ = biologically effective UV-B; $V_o$ = symplastic volume at full turgor; $z$ = tissue elasticity coefficient; $\varepsilon$ = tissue volumetric elastic modulus; $\varepsilon_{max}$ = tissue volumetric elastic modulus at full hydration; $\psi_{\pi 100}$ = symplastic osmotic potential at full hydration; $\psi_{lx}$ = leaf xylem pressure potential.

## Introduction

Decreases in the stratospheric ozone layer create the potential for increased ultraviolet-B (UV-B) radiation (280–320 nm) at ground level. Increases in UV-B may pose a hazard to natural aquatic and terrestrial ecosystems as well as suppress worldwide crop production, although the latter is increasingly in doubt (Fiscus et al., 1994; Fiscus and Booker, 1995).

Stomata, which control the plant interface with the gaseous environment, have a special role in plant responses to environmental stresses. Stomatal responsiveness to perturbations of leaf water balance are well known. Reports of stomatal responses to increased UV-B radiation, however, are not consistent and range from no effect (Brandle et al., 1977; Murali and Teramura, 1986; Sisson and Caldwell, 1976; Teramura et al., 1983) to both conductance decreases (Bennett, 1981; Björn, 1989; Murali and Teramura, 1986; Teramura et al., 1983) and conductance increases (Ogoeva, 1974; Teramura et al., 1983). Teramura et al. (1984) found no significant responses of leaf water potentials or leaf conductance in soybean to supplemental UV-B radiation unless the plants had been preconditioned with water stress. Decreases in fresh weight without accompanying decreases in dry weight in response to UV-B exposure (Krizek, 1981; Tevini et al., 1981) also suggest possible perturbations in the water relations of leaves subjected to elevated UV-B radiation. These latter observations, taken together with the reports of disturbed stomatal function, might be symptomatic of changes in bulk leaf water relations. It is surprising that there is little information available on the underlying leaf water relationships that may lead to, or reflect, these responses. The purpose of our experiment, therefore, was to examine the osmotic and turgor relations of fully expanded soybean leaves, through pressure-volume analysis, to determine if changes in the bulk leaf water relations are consistent with reported perturbations in stomatal function. For this experiment we used a soybean cultivar, Essex, that has been reported to be susceptible to UV-B damage (Krizek, 1981; Teramura et al., 1990).

## Materials and Methods

In 1990, soybean (*Glycine max* (L.) Merr. cv. Essex) was grown in 15-l pots in a 2 : 1 : 1 (by volume) mixture of soil, sand and Metro-Mix 220 (W. R. Grace Co., Cambridge, MA)[1] in open-top field chambers (Heagle et al., 1979) at Raleigh, NC, USA. Plants were watered daily and fertilized biweekly with «Peters Blossom Booster» (10-30-20 : N-P-K) (Grace-Sierra Horticultural Products Co., Milpitas, CA)[1] and three times during the season with «Peters STEM» soluble trace elements and micronutrient mix (Grace-Sierra Horticultural Products Co., Milpitas, CA)[1].

Low, medium, and high UV-B supplements were provided by banks of fluorescent lamps (model UVB-313, Q-Panel Co., Cleveland, OH)[1] suspended in the open-top chambers as previously described (Booker et al., 1992). Lamps in the low treatment were wrapped in polyester film to filter out radiation less than 315 nm. Lamp irradiance in the medium and high UV-B treatments was filtered with cellulose diacetate (0.13 mm thickness) to remove radiation below 290 nm. Lamp banks were kept at a constant height of 0.4 m above the canopy, and the irradiance was varied with fluorescent dimmer controls on the lamp ballasts.

Broad band erythemal meters (model 2D, Solar Light Co., Philadelphia, PA)[1] with a spectral response similar to that of the Robertson-Berger (R-B) meter were used to set the lamp bank irradiance levels each day, and a Robertson-Berger meter (Berger, 1976) was used to monitor solar UV continuously. Ambient and chamber irradiances also were checked with a UV-visible spectroradiometer (model 742, Optronics Laboratories, Inc., Orlando, FL)[1] equipped with a 3.7-m long quartz fiber optics cable and Teflon diffuser head. The spectroradiometer was calibrated with an NIST-traceable 200 W

tungsten-halogen lamp standard of spectral irradiance (model 220A, Optronics Laboratories, Inc., Orlando, FL)[1] driven by a current regulated power source (model 65, Optronics Laboratories, Inc., Orlando, FL)[1]. Wavelength calibration was checked periodically by comparison with Hg emission lines from a UVB-313 lamp. The broadband erythemal meters were calibrated against the spectroradiometer as previously described (Booker et al., 1992) and biologically effective UV-B irradiance (UV-$B_{BE}$) was calculated by applying Caldwell's generalized plant action spectrum (Caldwell, 1971), normalized to 300 nm, to the spectroradiometer scans.

Stratospheric ozone losses corresponding to the supplemental UV-$B_{BE}$ radiation levels were calculated from the radiative transfer model derived from Green (1983) by Björn and Murphy (1985). The model was extensively modified[2] for ease of use and flexibility and additional functions added for Caldwell's plant action spectrum and the CIE erythemal spectral sensitivity curve (McKinley and Diffey, 1987). The model predicted a clear sky total daily UV-$B_{BE}$ irradiance for 21 June of 5.45 kJ m$^{-2}$. An average daily solar UV-$B_{BE}$ of 4.88 ± 0.12 (s.d.) kJ m$^{-2}$ measured by the Robertson-Berger meter for the 30 d surrounding 21 June indicated acceptable agreement with the model. Also on 21 June, the daily supplemental UV-$B_{BE}$ irradiance in the three treatments was set to 0, 4.43, and 8.13 kJ m$^{-2}$ for the low (control), medium, and high UV-B treatments. Due to an average UV-B shading effect of the open-top chambers of 24 %, the total daily UV-$B_{BE}$ irradiance for the three treatments was 4.14, 8.57, and 12.27 kJ m$^{-2}$. The treatments thus corresponded to an increase in the $O_3$ column thickness of 15 % for the low treatment and decreases of 20 % and 35 % for the medium and high treatments. Supplemental UV-B treatments were administered as a constant daily addition over a 6 h period (0900–1500 EST), with the lamp output levels being set each day, from sowing to harvest. To compensate for seasonal changes in photoperiod and solar UV-B irradiance, the supplemental irradiance levels were adjusted biweekly and thus maintained relatively constant ozone column depletion simulations (Booker et al., 1992). At the end of the season, the actual exposure figures were refined according to the ground-based measurements provided by the R-B meter. Thus, over the entire experimental period, the mean daily UV-$B_{BE}$ irradiances were 3.02, 6.24 and 8.98 kJ m$^{-2}$. On overcast days the treatments were discontinued if the UV-$B_{BE}$ irradiance fell below 20 % of the maximum calculated for our location on 21 June for more than 30 minutes. Solar UV-$B_{BE}$ was evaluated every 2 h afterward, and treatments resumed if the overcast cleared.

Periodically throughout the season, leaf conductances were obtained in association with carbon exchange rates measured with a Ll-COR 6000 portable photosynthesis system (Ll-COR, Lincoln, NE)[1]. Growth data were also collected by sequential harvest to obtain, among other things, total leaf area, mean area per leaf and specific leaf weight (SLW) during the season. Additional details of the experimental design, plant cultural conditions, growth analysis, gas exchange, yield and exposure methodologies may be found in Miller et al. (1994).

Leaves for pressure-volume (P-V) analysis were taken from the fourth node from the apex of the main stem within 1.5 h after sunrise to assure a high water potential and to avoid the problems associated with rehydration (Meinzer et al., 1986). Leaves were enclosed in a plastic bag containing a moist paper towel and severed from the plant. Leaves were placed in a pressure chamber (Soil Moisture Equipment Corp, Santa Barbara, CA)[1], which was lined with moist paper toweling, within 5 minutes after cutting. After the initial bal-

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[1] Mention of a product or company name does not constitute an endorsement or recommendation by the United States Department of Agriculture.

[2] Copies of the executable files on a computer disk may be obtained from EF at no charge.

ance pressure was determined, the leaf was over-pressurized for 15 to 20 minutes. Pressure was then brought below the previous balance pressure and the expressed sap, which had been collected on absorbent material in contact with the cut petiole surface, was weighed. The new equilibrium balance pressure then was obtained. This sequence was repeated a sufficient number of times to obtain a complete P-V curve as determined by on-line data plots. The Balance Pressure (BP)-Expressed Volume ($V_E$) data pairs were then analyzed according to the following model:

$$\psi_{lx} = -BP = -\frac{RTN_S}{V_O - V_E} + P_{MAX}\exp(-zV_E) \qquad (1)$$

Where $\psi_{lx}$ is the leaf xylem pressure potential; R, the gas constant; T, the temperature in Kelvins; $N_s$, the number of osmols of solute in the symplast; $V_o$, the original symplastic volume; $P_{MAX}$, the turgor pressure at $V_o$; and z, the tissue elasticity coefficient. The first term on the right side of the equation describes the osmotic relations of the tissue and was derived by Tyree and Hammel (1972). The second term was first used by Hellkvist et al. (1974) to describe the relationship between turgor and symplastic volume.

Data were fitted by a nonlinear least squares program as described by Fiscus et al. (1995) to obtain the coefficients presented in this paper. The procedure generates values of $P_{MAX}$ and $V_o$ that represent the fully hydrated condition of the leaf.

Following determination of the four coefficients in the equation, additional calculations were performed according to Fiscus et al. (1995) to find the so-called turgor loss potential (TLP) and the relative symplastic volume at that potential ($RSV_{TLP}$).

Tissue volumetric elastic modulus is a more widely used elasticity term than z and is usually defined as $\varepsilon = V(dP/dV)$ (Hellkvist et al., 1974). According to Sinclair and Venables (1983) and Fiscus et al. (1995), $\varepsilon$ can be expressed in terms of equation 1 as

$$\varepsilon = (V_O - V_E)\, z\, P_{MAX}\exp(-z\,V_E) \qquad (2)$$

With the tissue at full hydration ($V_E = 0$), equation 2 simplifies to $\varepsilon_{max} = -V_o z P_{MAX}$ or $\varepsilon_{max} = -zRTN_s$. Further discussion of the relationship between z and $\varepsilon$ may be found in Fiscus et al. (1995) and we mention it here only to remind the reader that such physical expressions as the volumetric elastic modulus can be influenced by both osmotic and turgor parameters.

The experiment was a completely randomized design of 3 replicates and 3 levels of UV-B (Low, Medium, High) for a total of 9 open-top chambers. Chambers were sampled four times throughout the experiment by sampling one plant from each of the 9 chambers during each of the four sampling periods. Due to the time required for the pressure-volume processing, each sampling period lasted 12 d. The sampling sequence among the treatments was randomized for each period to minimize temporal bias in the data. Individual plants were sampled only once. All parameters within each sampling period were compared by analysis of variance and by the Student-Newman-Keuls pairwise comparison. Differences were deemed not significant if P > 0.05.

## Results and Discussion

### Developmental Changes

The effects of plant age on the parameters for leaf water relations generally were greater than the effects of the UV-B treatments (Table 1). The integrated effect of normal ontological changes in parameters of leaf water relations is shown in figure 1 where potential-volume lines were calculated from the fitting coefficients in table 1. Seasonal variations in the
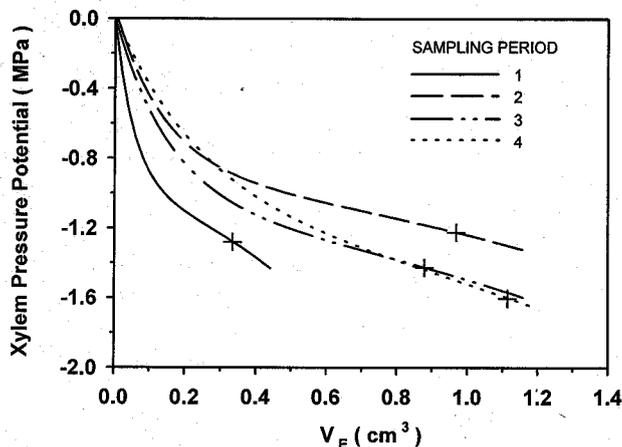


**Fig. 1:** Normal ontological changes in leaf pressure-volume relationships over the course of the experiments. Each line was calculated from equation 1 using the relevant mean values from table 1. Lines are terminated at $V_E \simeq V_o/3$. TLPs, calculated from the mean coefficients in table 1, are indicated by the crosses on the lines.

pressure-volume curves (Fig. 1) appear to be dominated by z and $\psi_\pi$, but predicting the shape of the P-V curve from these two parameters is not an obvious process since $\psi_\pi$ clearly influences the expression of z. For example, as a result of the large change in z between periods 1 and 2 that is accompanied by little change in $\psi_{\pi 100}$ ($-P_{MAX}$) (Table 1), the initial slope of the curve, in the region dominated by turgor changes, is less steep in period 2 than in period 1 (Fig. 1), and little change occurs in TLP. In contrast, the further increase in z between periods 2 and 3 is accompanied by a decrease in $\psi_{\pi 100}$. This combination of changes results in an initial slope of period 2 that appears less steep than period 3, even though z is lower in period 2. TLP, however, decreases in this instance. The effects of further increases in z and decreases in $\psi_{\pi 100}$ in the fourth period result in the least steep initial slope and a line that converges with the period 3 line at high levels of water loss.

Another especially noticeable feature in figure 1 is that the large increase in absolute quantities of water loss necessary to reach TLP can be attributed directly to larger leaf size and increased elasticity even though there is a seasonal trend toward decreasing TLP. Further discussion of the normal ontological changes may be found in Fiscus et al. (1995).
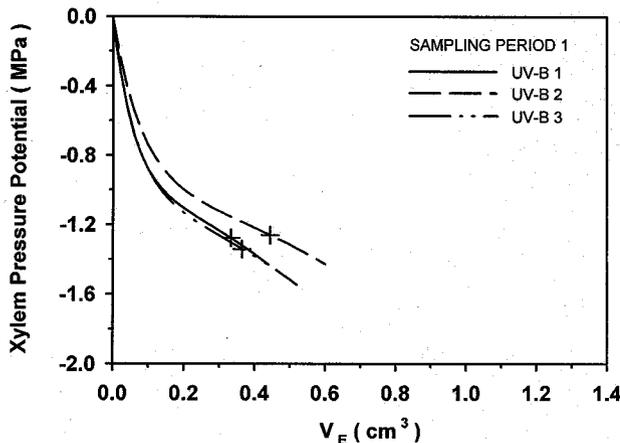
### Supplemental Ultraviolet-B

Among the parameters in table 1, a statistically significant response to the UV-B treatments occurred only for $V_o$, z and $RSV_{TLP}$. During period 2 $V_o$ was significantly reduced by the highest UV treatment, while during the same period z was significantly less in the medium and high UV treatments than in the low treatment. Again, in the fourth period, z was significantly less in the high treatment than the medium but did not differ from the low treatment. The only other significant difference occurred during the fourth period when $RSV_{TLP}$ was larger in the high UV treatment. In this case, the differences (Table 1) are due to normal ontological declines

**Table 1:** Means comparison of soybean leaf parameters. Numbers in parentheses in sampling period column are the mean days after planting ($DAP_0$ = day 151 of 1990) for that period. SLWs are the means for all the leaves on the plant (n=4 plants) and Leaf Area is the mean area per leaf of all the leaves on the plant (n=4 plants). For all the osmotic and turgor parameters, n=3. UV-B treatment numbers correspond to low (1), medium (2) and high (3) exposure levels. Numbers in a column in the same sampling period are not different at the $P<0.05$ level if followed by the same letter.
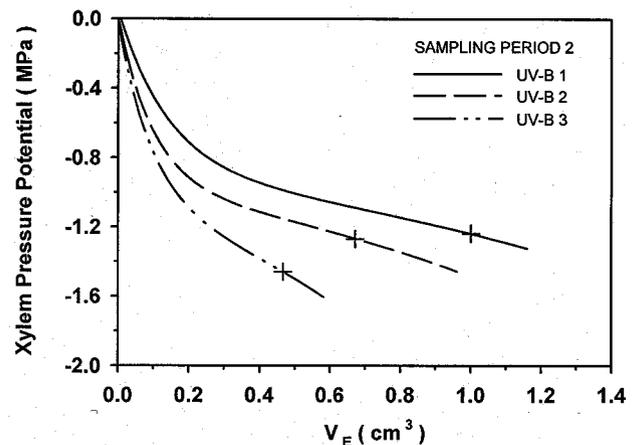
| Sampling Period | UV-B Treatment | $V_0$ cm$^3$ | z cm$^{-3}$ | $P_{MAX}$ MPa | $N_S$ mosmol | TLP MPa | $RSV_{TLP}$ | SLW mg cm$^{-2}$ | Leaf Area cm$^2$ |
|---|---|---|---|---|---|---|---|---|---|
| 1 (38) | 1 | 1.34a | −18.1a | 0.96a | 0.52a | −1.28a | 0.751a | 3.52a | 57.0a |
|  | 2 | 1.81a | −12.6a | 0.94a | 0.70a | −1.26a | 0.755a | 3.36a | 51.0a |
|  | 3 | 1.54a | −15.2a | 0.98a | 0.64a | −1.34a | 0.763a | 3.56a | 57.5a |
| 2 (58) | 1 | 3.51a | −7.00a | 0.93a | 1.32a | −1.22a | 0.767a | 3.48a | 125.7a |
|  | 2 | 2.91ab | −9.90b | 0.98a | 1.14a | −1.24a | 0.790a | 3.27a | 145.2a |
|  | 3 | 1.81b | −10.19b | 1.07a | 0.80a | −1.46a | 0.729a | 3.38a | 133.2a |
| 3 (72) | 1 | 3.54a | −6.28a | 1.08a | 1.54a | −1.43a | 0.752a | 3.95a | 118.2a |
|  | 2 | 3.26a | −7.33a | 1.00a | 1.32a | −1.33a | 0.756a | 3.84a | 120.3a |
|  | 3 | 3.84a | −6.57a | 1.03a | 1.61a | −1.34a | 0.771a | 3.99a | 108.5a |
| 4 (100) | 1 | 3.62a | −3.90ab | 1.13a | 1.63a | −1.62a | 0.694a | 4.30a | 117.1a |
|  | 2 | 4.62a | −3.23a | 1.23a | 2.28a | −1.74a | 0.703a | 4.26a | 130.6a |
|  | 3 | 3.46a | −6.24b | 1.21a | 1.71a | −1.62a | 0.751b | 4.49a | 118.8a |

that did not occur in the high UV treatments. Changes in the P-V parameters generally were small compared to the normal ontological changes recorded over the four sampling periods. Specifically, while the difference in $V_0$ between the medium and the high UV treatment was 48 % in period 2, the seasonal change was 2.7-fold, and corresponding values for z were 31 % and 4. 6-fold.

Integration of all the parametric changes are shown in figures 2–5. The curves in figure 2 (period 1; about mid-vegetative phase) differ primarily because of the non-significant difference in z, although there is little difference in the absolute quantities of water loss to TLP. During period 2 (Fig. 3; early reproductive phase), however, the decreasing values of both $V_0$ and z with increasing UV-B affect the shape of the curves, which indicate a substantial decrease in the total



**Fig. 3:** Changes induced in the leaf pressure-volume relationships by UV-B treatment at sampling period 2. Each line was calculated from equation 1 using the relevant mean values from table 1. Lines are terminated at $V_E \simeq V_0/3$. TLPs, calculated from the mean coefficients in table 1, are indicated by the crosses on the lines.

water loss necessary to reach TLP at the medium and high UV-B levels. Period 3, which occurred during the mid-reproductive stage (Fig. 4), showed no significant effects of the UV-B treatments. Finally, the shape of the curves in period 4 (Fig. 5; late reproductive phase) reflect the lower value of z and the higher $RSV_{TLP}$ under high UV-B as indicated in table 1.

Although measurements were not available for the first sampling period, there was no significant effect of UV-B on stomatal conductance over the remainder of the season starting at a time corresponding to period 2 (Fig. 6). Neither was there a detectable effect on carbon exchange (Miller et al., 1994; Fiscus et al., 1994), nor were there any differences in total leaf area (Miller et al., 1994), mean area per leaf (Table 1) or SLW (Table 1).



**Fig. 2:** Changes induced in the leaf pressure-volume relationships by UV-B treatment at sampling period 1. Each line was calculated from equation 1 using the relevant mean values from table 1. Lines are terminated at $V_E \simeq V_0/3$. TLPs, calculated from the mean coefficients in table 1, are indicated by the crosses on the lines.

The lack of significant changes in the present experiment concurs with the conclusions of Teramura (1983) that SLW is not a reliable indicator of UV-B stress. While Teramura (1983) also stated that leaf area generally is reduced by UV-B treatments, our results do not show such an effect (see also Miller et al., 1994). Changes in $V_o$, however, may be interpreted as changes in leaf size, and we did observe a statistically significant transient reduction of about 48 % (Table 1) during period 2 at the highest UV-B exposure. Since the symplastic solution constitutes the bulk of the leaf fresh weight and in the absence of any change in SLW or leaf area, the decrease in $V_o$ during period 2 is consistent with the observations of Krizek (1981) and Tevini et al. (1981).

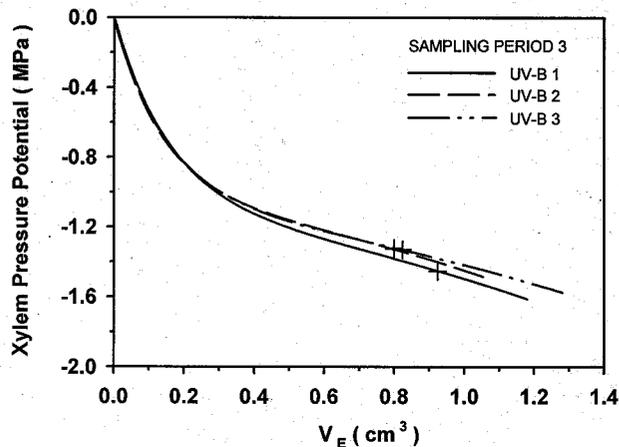Although a review of previous experiments by Fiscus and Booker (1995) has shown a consistent occurrence of UV-B



Fig. 6: Leaf conductance measured during carbon exchange measurements during the season. None of these data show any differences at the $P<0.05$ level of significance.

induced phenylpropanoid metabolism and synthesis of UV-B absorbing compounds, it seems unlikely that changes in $V_o$ and z are related to the production of soluble phenolics. In the absence of changes in SLW, it also is unlikely that the differences in elasticity would be due to deposition of additional lignin. Furthermore, there is no evidence that UV-B induces lignin synthesis. It is possible, however, that elasticity differences were due to changes in conformation and cross linking of cell wall phenolics and proteins induced by UV-B (see also Caldwell et al., 1989).

In conclusion, UV-B irradiation treatments resulted in only sporadic changes in $V_o$ and z that noticeably affected the overall leaf P-V relationships. However, these effects were small compared to normal ontological changes and were not sufficient to disturb the leaf water balance in such a way as to affect conductance, gas exchange or eventual yield, despite the severity of the treatments.
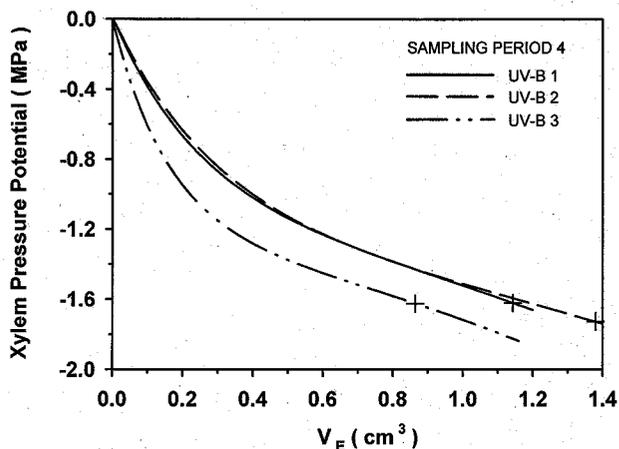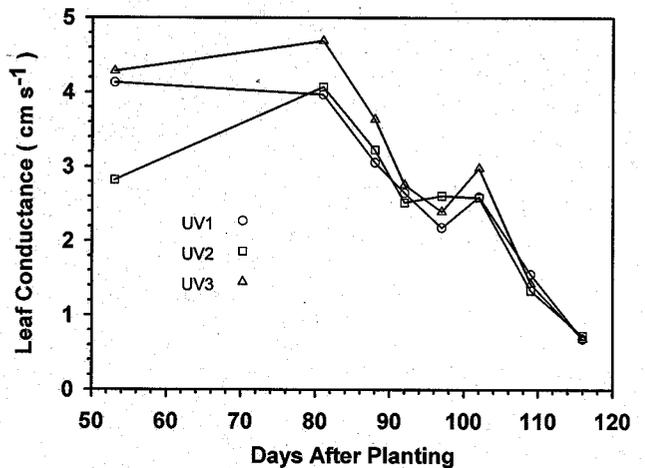


Fig. 4: Changes induced in the leaf pressure-volume relationships by UV-B treatment at sampling period 3. Each line was calculated from equation 1 using the relevant mean values from table 1. Lines are terminated at $V_E \simeq V_o/3$. TLPS, calculated from the mean coefficients in table 1, are indicated by the crosses on the lines.



Fig. 5: Changes induced in the leaf pressure-volume relationships by UV-B treatment at sampling period 4 Each line was calculated from equation 1 using the relevant mean values from table 1. Lines are terminated at $V_E \simeq V_o/3$. TLPs, calculated from the mean coefficients in table 1, are indicated by the crosses on the lines.

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