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Digital measurement of heliotropic leaf response in soybean cultivars and leaf exposure to solar UVB radiation

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Abstract

Inconsistencies in reported sensitivities of soybean cultivars [*Glycine max* (L.) Merr.] to enhanced ultraviolet-B (UVB) irradiance may in part be due to differences in the radiative environment of the experimental conditions or differences in exposure due to heliotropic response. In order to examine the impact of heliotropic movement on UVB exposure of the soybean upper trifoliate, leaf position was electronically recorded and inclination and azimuthal position of the leaves calculated for three soybean cultivars—Bay, York, and Williams 82—under greenhouse and field conditions. The UVB exposures of the top trifoliate of three soybean cultivars were modeled using anisotropic and isotropic sky radiance distributions. The Williams 82 cv. produced the greatest variation in leaf angle with solar zenith angle of the three cultivars, averaging between 19 and 47°, compared with a lower 10–27° range for York and Bay cultivars. The incidence angle data for the upper trifoliates of the field plants were not significantly different from the greenhouse plants. For clear sky conditions, overall exposure differences indicated that the Bay cultivar receives more UVB than the York or Williams 82 cultivars, in large part due to the higher variation in heliotropic movement shown by the Bay cultivar in response to the sun location.

Keywords: Soybean; UVB exposure; Leaf orientation; Radiation partition; Digital measurement

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1. Introduction

In recent years, increased ultraviolet-B (UVB) radiation levels due to decreased ozone column thickness (Molina and Rowland, 1974) have raised awareness of the effects of UVB on the terrestrial ecosystems. Ultraviolet (UV) radiation generally has a deleterious effect on plants, often producing reductions in leaf area and plant growth (e.g. Caldwell, 1971; Biggs et al., 1981; Reed et al., 1992), plant productivity (e.g. Teramura and Murali, 1986; Rosa and Forseth, 1995; Lydon et al., 1986), photosynthesis (e.g. Sisson and Caldwell, 1977; Teramura and Caldwell, 1981) and damage to DNA (e.g. D'Surney et al., 1993). With increasing UVB radiation levels, greater plant tolerance to UVB is essential to maintain yield levels in food crops such as soybean.

The sensitivity of soybean [*Glycine max* (L.) Merr.] cultivars to enhanced ultraviolet-B (UVB) irradiance varies widely, with many studies producing contradictory conclusions. Teramura and Murali (1986) found that, from a study of the five cultivars—Bay, York, Williams, Essex, and Forrest—Forrest cv. was the most ultraviolet (UV) tolerant whereas Williams and Essex cultivars were the most UV-sensitive. Alternatively, Murali et al. (1988) compared the UV

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sensitivities between Essex and Williams cultivars. The data showed that Essex was sensitive to UV in the parameters of leaf area, total plant mass, and specific leaf weight, whereas Williams was unaffected by UV and in fact showed an increase in specific leaf weight and UV-absorbing compounds. Lydon et al. (1986) observed changes in sensitivity to UVB with plant development and found that the physiological (growth and productivity) response of the plant was specific to the cultivar and dependent on UV exposure. Their results showed that Essex, Williams, Bay, and York cultivars were detrimentally affected by UVB, whereas James and Forrest cultivars were stimulated by exposure to UVB. Rosa and Forseth (1995) attributed higher UV-tolerance by Forrest cv. over Williams and Essex cultivars to the higher observed leaf inclination angles (30–75°) that were particularly evident over the midday hours. Although not directly comparable, physiological data of leaf area and leaf weight of Williams cultivars (as opposed to Williams 82 cv.) from Lydon et al. (1986) and Murali et al. (1988) demonstrated that Williams had a greater tolerance to UVB exposure than Bay and Essex, respectively. In a study of five cultivars—Forrest, Essex, Ogden, York and Dare—Wofford and Allen (1982) found that the degree of leaf inclination, and by implication UV exposure, varied with cultivar and the developmental stage of the plant. The inclination angles increased for all cultivars with maturity of the plant, for both the central and side leaves. Teramura et al. (1980) showed that low levels of photosynthetically active radiation (PAR) increase the effects of UV on plants.

Such inconsistencies in the sensitivities of the soybean cultivars may in part have been due to differences in the radiative environment of the experimental conditions. Some of the variability in reported sensitivity of soybean cultivars appeared to correspond to differences in exposure due to heliotropic response (Grant, 1999). Grant (1999) applied the model to the measured leaf orientations obtained by Rosa and Forseth (1995) with the result that Forrest cv. had the least UVB exposure, followed by Cumberland, Essex and CNS cultivars. The greatest exposures were in the morning and afternoon and decreased over midday, with calculated UVB exposures of 5.04, 5.60, 5.77 and 6.24 $\mathrm{kJ\,m^{-2}}$ for Forrest, Cumberland, Essex, and CNS cultivars, respectively. The decreased UVB exposure for Forrest cv. and correspondingly higher exposure for CNS cv. is indicative of the sensitivity of these cultivars to UVB irradiance.

Several previous studies of soybean leaf exposure to UVB assumed the leaves were a horizontal plane, for example Parisi et al. (1996), Murali et al. (1988), and Teramura and Caldwell (1981). In addition, the distribution of the UVB radiance over the sky hemisphere was either assumed constant over the whole sky (isotropic) or not considered, for example Murali and Teramura (1986), Mazza et al. (2000), Lydon et al. (1986) and Rosa and Forseth (1995). One of the aims of this paper was to examine in more detail how the soybean leaf angle varied over the day and how the changes in leaf angle affected the exposure of UVB received. The UVB exposure over the growing season and for clear, overcast, and hazy conditions was determined for assumed isotropic and anisotropic UVB sky radiance distributions to ascertain how these assumptions affected the UVB exposure on the soybean leaves.

The second aim of this paper was to further examine the impact of heliotropic movement on UVB exposure of the soybean upper trifoliate for three cultivars under greenhouse and field conditions. As the greenhouse glass did not transmit UVB radiation onto these plants, the data were compared to determine any differences in leaf angles and hence UVB exposure between the greenhouse and field groups.

2. Methods

2.1. Measuring the leaf angles

A Microscribe 3D inscriber (Immersion Corporation, San Jose, CA) was implemented to digitize the 3D inclination and azimuthal position of the leaves with greater precision than an inclinometer and compass. Measurements of leaf orientation were made using the Microscribe 3D-coordinate digitizing system; the order of points measured for a single trifoliate is displayed in Fig. 1A. The repeatability of any one point was found to have a 5° measurement error. Five points on each leaf of the upper trifoliate were digitized, three that follow the leaflet mid-rib (or leaf-spine), and two either side of the midpoint to mark the edges; the latter signified any folding of the

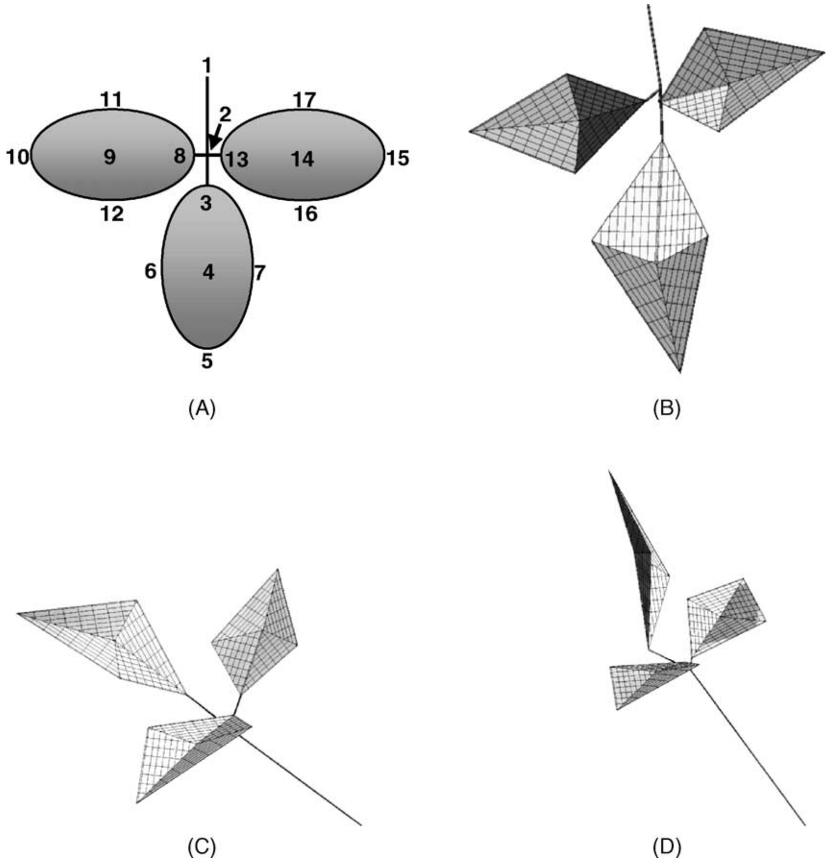

Fig. 1. Schematic diagram (plan view) in A showing the order of the points marked by the inscriber on each leaf of the top trifoliate. An example of a digitized trifoliate (plan view) from a Williams 82 plant is shown in B, and examples of a single Bay plant (cross-section view) demonstrating variations in inclination angle over the period of 1 h are shown in C and D.

leaf that could indicate water stress. Preceding the leaf points, two marker points indicate the position of the trifoliate stem on the main stalk and the junction of the three petioles and provide a starting position on each trifoliate. This combination results in quadrilateral leaf shapes that indicate the movements and variations in inclination and azimuth angles of the trifoliate (Fig. 1C and D).

2.2. In the greenhouse

During the spring and summer of 2001, three cultivars of soybean—Bay, York, and Williams 82—were grown in the greenhouse at West Lafayette, IN (40.5°N, 87°W). The top trifoliates from three plants of each cultivar were measured with the inscriber and data from each cultivar were averaged into two groups: those with the azimuth of the central leaflet within ±90° of the solar azimuth (“on-sun”) and “off-sun” for the remainder. Only data from clear-sky days and “on-sun” measurements will be discussed in this paper due to a low sampling rate in overcast conditions and low number of samples for the “off-sun” plant leaves. The growth stage (Fehr and Caviness, 1977), height of the top trifoliate, damage to the leaves, and local cloud conditions were recorded for each measurement period.

The leaf angle measurements in the greenhouse were recorded in the morning and afternoon hours. In the most part, this restricted comparisons between the field and greenhouse plants to an average of two measurements between 10:00 and 16:00 h. Data from the field plants were chosen at these two times and averaged over the 6 h period.

The measured light transmittance through the greenhouse glass panels was above 80% for wavelengths above 350 nm; below 350 nm the transmittance rapidly reduced to 10% at 320 nm and <1% at 310 nm. The UV irradiance was supplemented by UVA-340 and UVB-313 lamps (Q-Panel Lab Products, Cleveland, OH) that were positioned at a height of 1.1 m above the workbench. The mean daily UVA and UVB irradiance maxima were 14.1 and 3.7 $\mathrm{W\,m^{-2}}$, respectively at distance of 0.42 m from the UV lamp bulbs. As a safety measure, the measurement area was enclosed on two sides (north and west) with thick black plastic that transmitted no light at all wavelengths below 1200 nm. This reduced the natural light inside the measurement area by 10% that entailed the inclusion of sodium lamps to supplement the PAR output to a mean of 16 $\mathrm{mol\,m^{-2}}$ per day. The mean daily UVB irradiance inside the UV area during the growing period was 53 $\mathrm{kJ\,m^{-2}}$ per day and negligible in the control area, the UVA was 334 $\mathrm{kJ\,m^{-2}}$ per day inside the UV area and 221 $\mathrm{kJ\,m^{-2}}$ per day in the control area, and the PAR 16 $\mathrm{mol\,m^{-2}}$ per day inside the UV area and 25 $\mathrm{mol\,m^{-2}}$ per day in the control area—the UV area thus being 65% of the ambient PAR levels. The containers were positioned under the lamps at a separation of approximately 0.3 m to maximise the light incident on each plant due to the lower PAR levels in the UV area.

2.3. In the field

Williams 82, Bay and York soybeans were planted at West Lafayette, Indiana (40.48°N, 86.99°W) on May 30, 2001. For each cultivar, five rows were sown each of 9.1 m in length and spaced 0.7 m apart. Measurements of the top trifoliate of four plants of Williams 82 cv., six plants of Bay cv. and four plants of York cv. were recorded at hourly intervals between 8 a.m. to 5 p.m. (EST) for one cultivar per day from 11 to 13 September 2001, respectively. At this time, Bay and York were at full seed (R6) stage, with Williams beginning maturity at R7 (Fehr and Caviness, 1977). Weather conditions on the measurement days brought clear skies on the 11th, mostly clear with some cirrus on the 12th, and mostly clear that changed to partly cloudy then overcast after solar noon (Stratocumulus) on the 13th. For each cultivar, the measured plants were situated within 1 m of each other, were in the same soil type and showed no indication of water stress.

2.4. Data reduction

Leaf heliotropism was calculated using a reference line drawn along the leaf spine between the first and third points on each leaf of the top trifoliate, that is, between points 3 and 5, 8 and 10, and 13 and 15 (Fig. 1A). The leaf zenith angle θ_L, that is the angle between the leaf spine and the vertical, and the azimuth angle of the leaf spine from True North ϕ_L were calculated from the 3D-digitized data. The angle between the leaf spine and the horizontal plane, called the inclination angle α' (or $90 - \theta_\mathrm{L}$), and the angle between the normal $\hat{n}$ to the leaf plane and the solar incidence angle on the leaf plane, called the incidence angle Θ, were determined from these measurements (Fig. 2). The change in the solar incidence angle $\Delta\Theta$, the change in the leaf angle Ψ_L, and the percentage change between the leaf and sun angles ($\Psi_\mathrm{L}/\Psi_\mathrm{S}$) between hourly data were also calculated. The mean values of the above parameters per measuring period for each plant were compared between field and greenhouse data. Statistically significant values ($P = 0.05$) were determined using the student's *t*-test (Zar, 1984).

2.5. Modeling top trifoliate leaf angles

Models of the inclination and incidence angles of Williams 82, York and Bay cultivars were developed

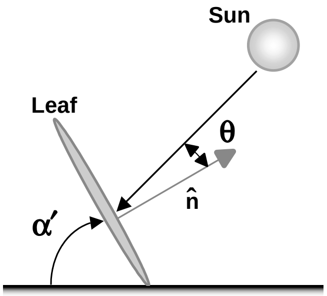

Fig. 2. Schematic diagram (cross-section) showing the angle between the leaf spine and the horizontal, or inclination angle α', and the angle between the normal $\hat{n}$ to the leaf plane and the solar incidence angle on the leaf plane, or incidence angle Θ.

as a function of solar zenith angle based on leaf orientation measurements made in the field. Due to the large amount of scatter data were averaged in five degree bins, for example (35–39.9°) and (40–44.9°), and the trend obtained from the means.

2.6. Modeling irradiance

Spectral and broadband UVB irradiances were measured at the Purdue Agronomy Farm site using two instruments that form part of the USDA UVB Monitoring Program Climatological UVB Network. Three-minute averaged spectral irradiance data over the soybean growth period from 1 May to 31 August 2001 were obtained from a YES (Yankee Environmental Systems, Turners Falls, MA) ultraviolet multi-filter rotating shadowband radiometer (UV-MFRSR) instrument and broadband UVB data from a YES UVB-1 radiometer. Grant and Gao (2002) found that the diffuse fractions across the entire UVB waveband were nearly constant, thus the broadband data were partitioned into direct normal and diffuse components using the direct-normal, global and diffuse data from the 311-nm channel of the spectral instrument.

2.7. Estimation of top trifoliate exposure

The UVB exposure of the upper trifoliate was determined using the partitioned measured UVB irradiance and modeled leaf orientations with the goal of evaluating the relative importance of the varying heliotropic response of three cultivars—Bay, York and Williams 82—to the received exposure.

The UVB exposure was calculated using Eq. (1) below and assumed a canopy reflectance of 1.5% (Grant, 1998). The total irradiance on the inclined leaf plane R_s was estimated according to:

$$R_s = g\, R_d 0.5\,(1+\cos\alpha') + R_b\cos\theta + (R_d + R_b)0.5\rho_{can}(1+\sin\alpha') \qquad (1)$$

where R_d is the diffuse irradiance, R_b is the direct beam irradiance, α' is the inclination angle of the leaf from a horizontal plane (above the plane is positive), ρ_{can} is the canopy reflectance, Θ is the solar incidence angle on the plane of the leaf, and g is the sky radiance distribution coefficient adjusting the diffuse irradiance for the sky radiance distribution (from Grant, 1999). The sky radiance distribution coefficients for anisotropic (ANISO) (Grant, 1999) and isotropic (ISO) ($g = 1$) clear sky radiance distribution models were used to determine whether the sky radiance distribution, which affects the diffuse irradiance on the leaf, significantly influenced the predicted exposure.

Since local irradiance measurements were used for the seasonal exposure estimates, the ozone column depth and cloud cover of the season were inherently included in the daily and cumulative exposure estimates.

3. Results and discussion

3.1. Trifoliate orientation measurements

The measured heliotropic response was complex and varied between cultivars. On average, Williams 82 cv. produced the greatest leaf movement Ψ_L with solar zenith angle of the three cultivars, averaging between 19 and 47° per hour, followed by York with 13–27° and Bay with 10–24°. The incidence angle Θ values for the upper trifoliate of the field plants were not significantly different (student's t-test, $P = 0.05$) from the greenhouse plants, while α' was significantly different for only the central leaflet of the Williams 82 cultivar (Table 1). An example of the extent of variation in the incidence angle on the central leaf of the upper trifoliate for three field plants is shown in Fig. 3. In this example, minimum Θ values of 50 and 36° for both York and Williams 82 cultivars occurred between 09:00 and 09:30 h whereas low Θ values for Bay cv. of 27 and 16° occurred both in the mid-morning and mid-afternoon hours. The central leaflet of the Bay cv. top trifoliate had inverted by 11:00 h but was restored by 14:00 h (Fig. 3), whereas the top trifoliate for York cv. inverted between 14:00 and 15:00 h. The variation in Θ over the course of the day and between cultivars was larger by 13° for Bay but smaller by 7° for York than the 21° incidence angle variation found by Rosa and Forseth (1995) for the pedigree-related Essex cultivar.

Mean inclination α'_m and incidence angle Θ_m data for the central leaflet (L1) and the mean of the two side leaflets $(L2, L3)_m$ of the greenhouse and field plants for Williams 82, Bay and York cultivars over the time interval 10:00–16:00 h for all clear sky measurement

Table 1
A comparison between the greenhouse (GH) and field plants for Williams 82, Bay and York cultivars, displaying the mean inclination α'_m and incidence angles Θ_m (in degrees) for the time interval 10:00–16:00 h for all clear sky measurement days

Cultivar	α'_m (deg)				Θ_m (deg)			
	L1		(L2, L3)$_m$		L1		(L2, L3)$_m$	
	GH	Field	GH	Field	GH	Field	GH	Field
Williams 82	24.3*	49.8*	26.5	32.9	62.0	59.3	62.7	49.4
Bay	38.8	23.3	35.3	25.8	57.6	64.7	66.3	65.9
York	26.2	24.1	31.1	22.4	57.2	63.1	54.3	60.8

Data are for the central leaflet L1 and an average of the side leaflets (L2, L3)$_m$ of the top trifoliate and are for "on-sun" measurements only. Significant differences (student's t-test, $P = 0.05$) between the field and greenhouse data are indicated with an asterisk (∗).

days are set out in Table 1. Significant differences (student's t-test, $P = 0.05$) occurred in one instance only—for the inclination angle of the central leaflet of the Williams 82 cultivar. This absence of significant differences in the incidence angle Θ between the field and greenhouse plants indicated that the greenhouse environment did not inhibit the heliotropic response of the soybean plants.

The inclination angle α' of the leaf spine for the central leaf of the top trifoliate versus solar zenith angle θ_s produced linear relationships for all three cultivars which differed in their individual responses to the sun. A decrease in α' with increasing θ_s for the central leaflet of York (Fig. 4A) from 27 to 19° and larger increase for the side leaflets (Fig. 4B) from 19 to 39°, combined with a small increase in the incidence angle for the central leaflet (63–68°) (Fig. 5A) and larger decrease on the side leaflets (75–43°) (Fig. 5B) indicated a slight avoidance of the central leaflet from the sun's rays, while the side leaflets were increasing the exposure on the leaves. An increase in α' with increasing θ_s for the central (Fig. 4C) (24–61°) and side leaflets (Fig. 4D) (25–32°) of Williams 82 cultivars combined with a very small decrease for the incidence angle on the central leaflet (60–52°) (Fig. 5C) and a small decrease in incidence on the side leaflets from 53 to 44° (Fig. 5D) indicated that this cultivar was increasing the exposure of all three trifoliate leaves relative to the leaf exposures for York and Bay. This near-constant incidence on the central leaflet and small decrease with solar zenith angle for the side leaflets suggested a high degree of heliotropy for the Williams 82 cultivar. The range of mean inclination angles for the Bay cv. was low for both the central leaflet (18–30°) (Fig. 4E) and side leaflets (25–15°) (Fig. 4F). The incidence angle decreased with increased solar zenith angle for the central leaflet (74–41°) (Fig. 5E) and increased (49–67°) for the side leaves (Fig. 5F), and this high degree of combined leaf movements for the Bay cv. indicated a lesser degree of heliotropic movement when compared to the Williams 82 cultivar.

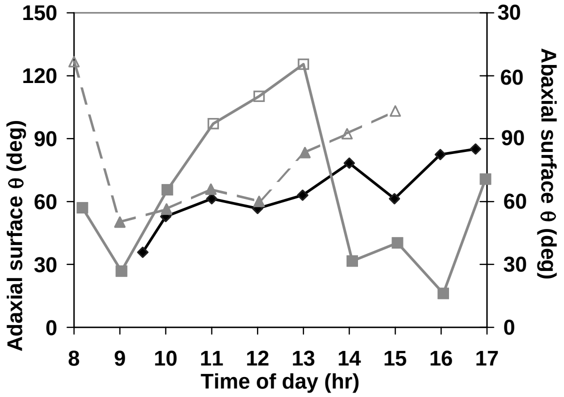

Fig. 3. Diurnal variations in the incidence angles Θ of the center leaflets of the top trifoliates of Williams 82 (solid black line, diamond), York (broken grey line, triangle) and Bay (solid grey line, square) cultivars from field data of 11–13 September 2001. Filled symbols below the 90 degree line and open symbols above the line represent the incidence angles for the adaxial and abaxial sides of the leaf, respectively.

The higher degree of scatter in the mean inclination angle α'_m with θ_s shown for Williams 82 cv. over that of the York and Bay cultivars indicated that a more complex process controlled the leaf movement of Williams 82 (Fig. 4C). For this reason, more data were needed to indicate what might occur at lower and higher solar zenith angles for this cultivar. As the field and greenhouse inclination angle data were not

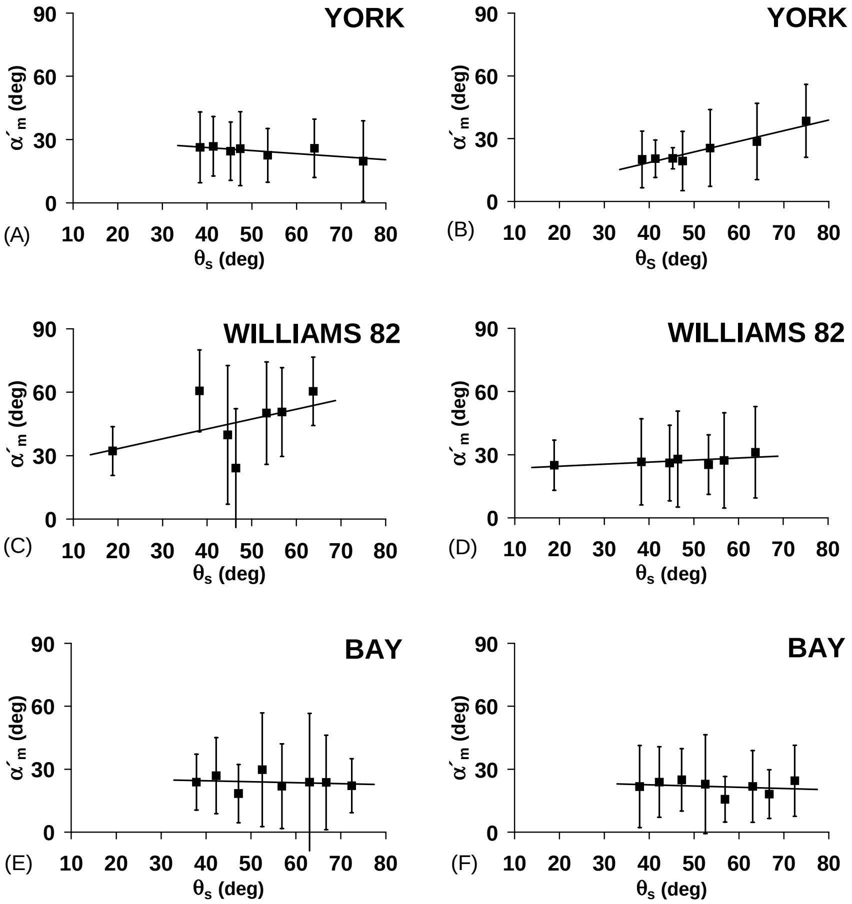

Fig. 4. Mean inclination α'_m angles (of the 5° bins) with solar zenith angle θ_s for York (A, B), Williams 82 (C, D) and Bay (E, F) from the field data from September 2001. The central leaflet data are in the left-hand column; data from the side leaflets are in the right-hand column. The bars indicate the standard deviation.

significantly different for all but one leaflet (Table 1), the inclination angle measurements of Williams 82 plants from the greenhouse recorded in late May and early June were included with the field measurements to reveal the leaf orientation at the lower solar zenith angles, as shown in Fig. 4(C,D) and Fig. 5(C,D).

The Williams 82 cultivar showed the greatest variation relative to θ_s in the mean inclination angle of the central leaflet of the top trifoliate (Table 2). The only range in inclination angles that were nearest to the 55° nominal exposure angle of Oosterhuis et al. (1985) were for the central leaflet of the Williams 82 cv., whereas all other leaflets showed inclination angles of less than 40°. The incidence angles for the top

Table 2
Range of inclination α'_m angles and incidence angles Θ_m, in degrees, for the central and side leaflets of the top trifoliate obtained from the field data for the Williams 82, York and Bay cultivars using the five degree averaged bin groups

Cultivar	α'_m (deg)		Θ_m (deg)	
	Central leaf	Side leaves	Central leaf	Side leaves
Williams 82	24–61	25–32	52–60	44–53
York	19–27	19–39	55–73	43–75
Bay	18–30	15–25	41–74	49–67

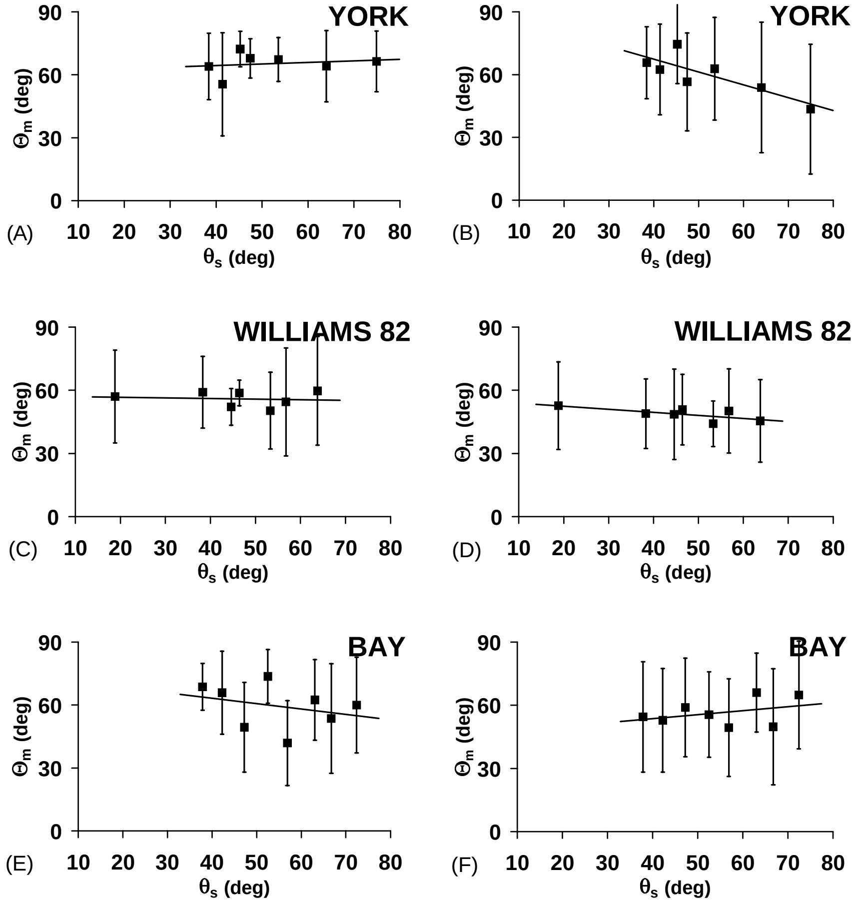

Fig. 5. Mean incidence angles Θ_m with solar zenith angle θ_s for the central and side leaflets of the top trifoliates for York (A, B), Williams 82 (C, D) and Bay (E, F) from the field data from September 2001. Data are displayed as in Fig. 4.

trifoliate of the Williams 82 cv. displayed the smallest variation; 52–60° for the central leaflet and 44–53° for the side leaflets. The incidence angles for the top trifoliates of the Bay and York cultivars showed a much larger variation, with variations above 30° for the central leaflet of Bay (41–74°) and side leaflets of York (43–75°), and 18° variations for the side leaflets of Bay (49–67°) and central leaflets of York (55–73°). As the York and Essex cultivars feature strongly in the Bay pedigree (USDA, ARS website, 2002), it was expected that Bay would exhibit similar properties to the York cultivar. A comparison between the inclination and incidence angles between Bay and York showed that the range of values overlapped for these two cultivars, and indicated that for these two variables the phenotype expressions of leaf movement and orientation were similar.

3.2. Comparison of cultivars

3.2.1. Inclination angle

The heliotropic movements of Essex cultivars were not measured in the field, but due to the similarities in their pedigrees (USDA, ARS website, 2002) York cv., and especially Bay cv., were expected to show similar characteristics to those reported by Rosa and Forseth (1995) for the Essex cultivar. The mean hourly inclination angles α'_m for the central leaflet of the field plants of York cv. (Fig. 6A) and Bay cv. (Fig. 6E) were much lower across the day than that found by Rosa

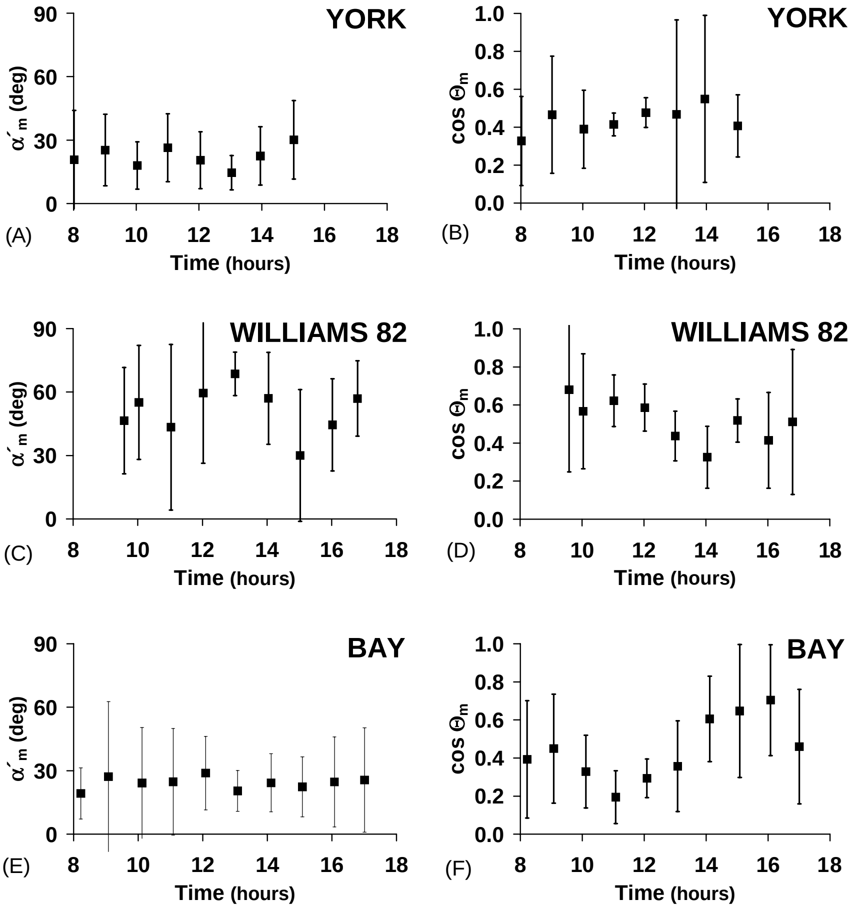

Fig. 6. Mean hourly data for inclination $\alpha'_{\rm m}$ (left column) and cosine of the incidence angles $\Theta_{\rm m}$ (right column) for York (A and B), Williams 82 (C and D) and Bay (E and F) cultivars from the field measurements. Data are for "on-sun" values only. The bars indicate the standard deviation per hour.

and Forseth (1995) for the Essex control group. There was no pronounced decrease in inclination angle near solar noon as shown in the Essex data, and very little deviation from the 15–39° range for all leaflets of the York and Bay cultivars than the larger 25–65° range for Essex. The differences may be due to the lower solar zenith angles at solar noon of 19° encountered in July for the Essex data of Rosa and Forseth (1995), compared with solar zenith angles around 36° at solar noon for the September data from the West Lafayette field site. In comparison, the change in inclination angle for the Williams 82 cultivars (Fig. 6C) shows a more sinusoidal-type variation over the course of the day, with a 70° mean inclination angle near solar noon (13:00 h) that dips at 11:00 and 15:00 h to between 30 and 45°. This type of sun-avoidance response during the solar noon hour is similar to that found by Rosa and Forseth (1995) for UVB-tolerant plants. York and Bay cultivars showed a decrease in inclination angle at solar noon, and data from Lydon et al. (1986) revealed that these plants were physiologically less tolerant to UVB exposure with smaller leaf areas and lighter leaf weights.

Another possible explanation for the inclination angle differences between the two studies could be due to differences in temperatures and water availability. With increased temperatures and reduction in water supply, soybean leaf movements become more paraheliotropic in order to avoid maximum solar radiation exposure on the leaf surface. In addition, previous studies by Berg and Hsiao (1986) and Fu and Ehleringer (1989, 1991) found that even well-watered plants can exhibit paraheliotropism near solar noon on hot, sunny days. In the greenhouse and field measurements in Indiana, the temperatures ranged from 25 to 38 °C in the greenhouse and 17–29 °C in the field. For these two locations there was an adequate water supply to the plants and any solar avoidance techniques by the trifoliates would be attributed more to heat stress than to water stress. A higher ambient temperature range of 27–37 °C in the field, and hence a greater tendency of the plants for solar avoidance, may explain the larger inclination angles in the measurements by Rosa and Forseth (1995) for the Essex cultivar than those measured for York and Bay cultivars in Indiana.

3.2.2. Incidence angle

The field data produced an almost sinusoidal diurnal variation in the cosine of the mean hourly incidence angle Θ_m, the second term in Eq. (1), for both York (Fig. 6B) and Bay (Fig. 6F) cultivars; York being to a less pronounced degree than Bay. While York and Bay are related in pedigree to the Essex cv., the diurnal variation in Θ_m differs. The Θ_m minima for York and Bay occurred in the late afternoon, between 14:00 and 16:00 h, compared with the Rosa and Forseth (1995) data that showed the minimum Θ_m angle for Essex cv. was at noon, and overall the Essex cv. data showed smaller incidence angles than those measured for the Bay and York cultivars. The maximum Θ_m for Williams 82 occurred an hour after solar noon at 1400 h, whereas low Θ_m values were recorded during the morning hours (Fig. 6D). The range in Θ_m for all three leaflets of the top trifoliate of Williams 82 cv. (44–60°) was less than Essex cv. (39–60°) recorded by Rosa and Forseth (1995), and half that of York (43–75°) and Bay (41–74°) cultivars (Table 2). This high degree of variation in Θ_m for the Bay and York cultivars indicated that these two cultivars showed the least degree of heliotropism out of the three cultivars studied.

3.2.3. Hourly angle changes

The hourly-averaged leaf angles Ψ_L and hourly-averaged Ψ_L/Ψ_S ratios for the “on-sun” field data are displayed in Fig. 6. Leaf angle data for York and Bay cultivars ranged between 11 and 33° (Fig. 7A and E, respectively) with means of 19.8 and 19.4, respectively. Both cultivars showed an increase in the leaf movement between 12:00 and 14:00 h that coincided with the increase in incidence angle for both cultivars. Leaf angles for Williams 82 cv. were higher (Fig. 7C), ranging from 19 to 47° (mean 28.7°), and, with the exception of a decrease between 13:00 and 14:00 h, showed a steady increase throughout most of the day until the late afternoon. This high degree of leaf movement supports the smaller variation in incidence angles achieved by this cultivar. The ratios of mean hourly leaf to sun angles for the Williams 82 cultivar were higher overall than those of Bay or York, with a mean of 2.10 and a range between 1.4 and 3.2 (Fig. 7D) that indicated that the leaf movement is on average more than twice the rate of movement of the solar disk. The mean ratios for Bay and York were 1.35 (range 0.6–2.6) (Fig. 7F) and 1.30 (range 0.6–1.9) (Fig. 7B), respectively, reiterating the higher degree of leaf movement for the Williams 82 cultivar.

3.2.4. Calculations of exposure

The measured broadband UVB horizontal above-canopy exposure over the May to August 2001 growing season was 6.06 MJ m^{-2}, with an estimated 4.68 MJ m^{-2} (77%) of the exposure due to the diffuse sky component and 1.38 MJ m^{-2} (23%) for the direct component.

The UVB exposures of the top trifoliates of three cultivars for the entire growing season were estimated assuming the heliotropic responses described previously for both cloudy and sunny days. Exposure estimates were calculated using both the assumption of isotropic sky radiance distributions (ISO) and anisotropic sky radiance distributions (ANISO) (Table 3). Assuming an anisotropic sky radiance distribution, the Bay cv., with the largest variation in the heliotropic response of the three cultivars, had the greatest exposure to the UVB over the course of the season, receiving a total of 5.63 MJ m^{-2}; 93% of the seasonal exposure of the horizontal plane. The most heliotropic cultivar, Williams 82, received 5.48 MJ m^{-2} (90% of the horizontal exposure), while the York cv., which showed a large variation in heliotropic response particularly in the side leaflets, had the lowest UVB exposure at 5.38 MJ m^{-2} (88% of the horizontal exposure).

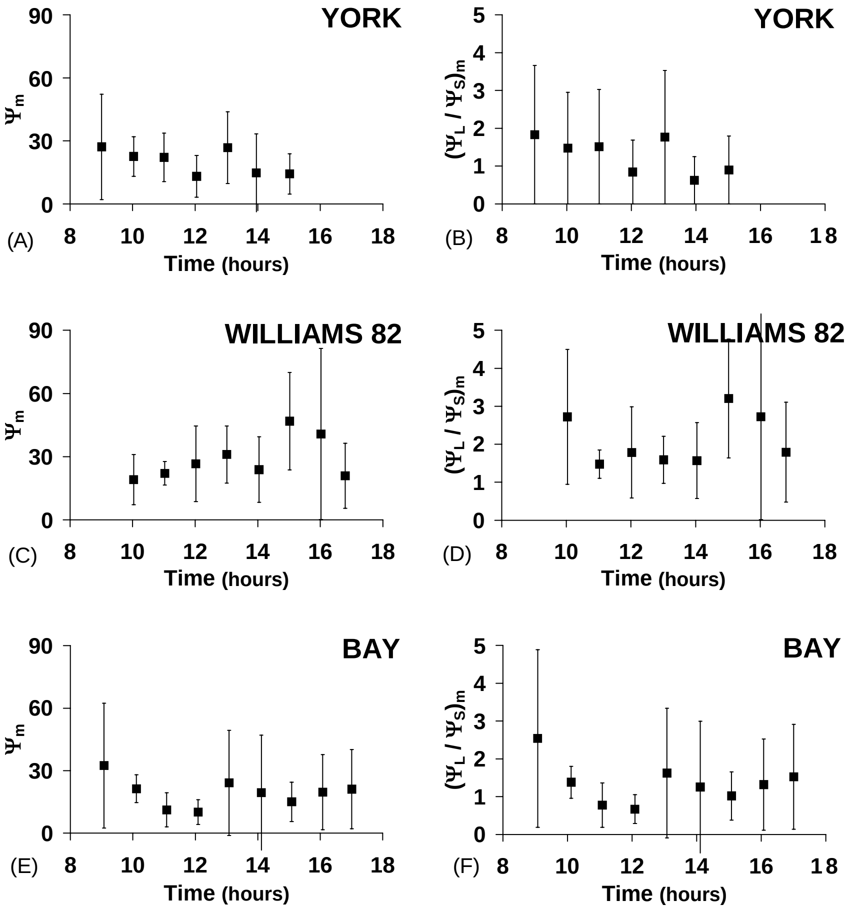

Fig. 7. Mean hourly change in the leaf angle Ψ_m for York (A), Williams 82 (C) and Bay (E) cultivars for the field plants. The mean ratios between the change in leaf and sun angles, $(\Psi_L/\Psi_S)_m$ are displayed for York (B), Williams 82 (D) and Bay (F) cultivars. The bars represent the standard deviation per hour. All leaf angle data are in degrees, the $(\Psi_L/\Psi_S)_m$ data are in degrees(leaf)/degrees(sun).

Table 3
Comparison between the ISO and ANISO sky radiation distribution models for calculating the UVB exposure received by the soybean leaves using the field exposure data (in MJ m^{-2}) for May to August 2001

Cultivar	Sky radiance distribution model					Horizontal exposure (MJ m^{-2})
	ISO (MJ m^{-2})	Percent of total	ANISO (MJ m^{-2})	Percent of total		
Bay	5.25 ± 0.2	86	5.63 ± 0.3	93	Total	6.06
Williams 82	5.17 ± 0.2	85	5.48 ± 0.3	90	Diffuse	4.68
York	5.00 ± 0.2	82	5.38 ± 0.3	88	Direct	1.38

The measurement error is included in the ISO and ANISO results.

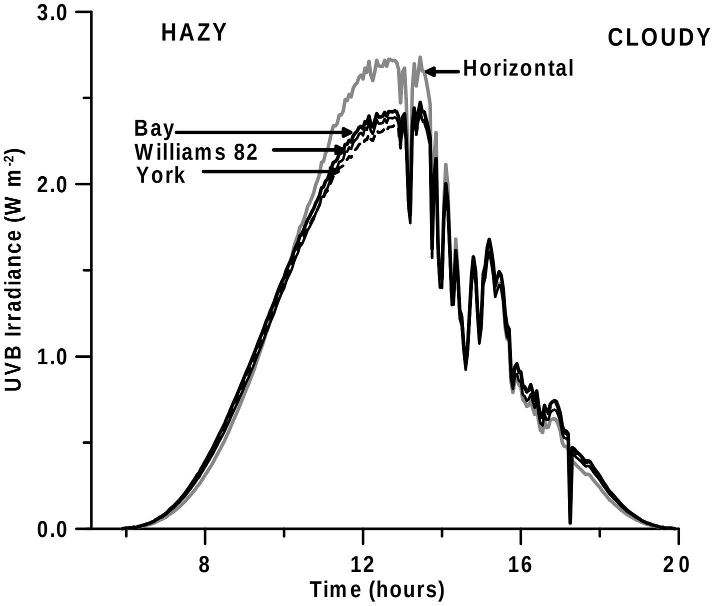

Fig. 8. UVB irradiance on the top trifoliate of Williams 82 (solid thin line), Bay (solid thick line) and York (dotted line) soybean cultivars on August 8, 2001 in hazy/partly cloudy conditions. The individual UVB irradiances were calculated using the ANISO model and are indicated by arrows for each cultivar. The UVB irradiance for horizontal leaves is displayed as the solid grey line.

Estimating leaf exposure based on the simpler isotropic assumption of diffuse sky radiance resulted in a UVB exposure that was between 4 and 7% lower than estimated using the previously developed anisotropic sky corrections to the diffuse sky model (Grant, 1999). The isotropic calculations produced exposures on Bay cv. of 5.25 MJ m^{-2} (86% of the horizontal exposure), Williams 82 cv. of 5.17 MJ m^{-2} (85%) and York cv. of 5.00 MJ m^{-2} (82%).

The sky condition during exposure influenced the relative exposure of the top trifoliate of all the three cultivars. A comparison was made between 3 days of differing sky conditions—clear sky, hazy and cloudy—from the 2001 data and results are displayed in Fig. 8 and Table 4. Under clear sky conditions (July 11) and an assumed anisotropic (ANISO) sky radiation distribution, the daily exposures of Bay and Williams 82 cultivars were almost equal, and exceeded the exposure of York cv. by 13.2% (Table 4). Under hazy conditions (August 8) and assumed anisotropic sky radiation distribution, the daily exposure of the Bay cv. exceeded that of the Williams 82 and York cultivars by 3.8 and 2.3%, respectively (Table 4, and illustrated in Fig. 8). Using an isotropic (ISO) distribution of sky radiation for the mostly overcast day (June 21), the estimated exposures of the top trifoliate of both the Bay and York cultivars exceed the Williams 82 cv. by 3.5 and 4.2%, respectively (Table 4). The 5° measurement error of the digitizing instrument produced experimental errors in the calculated UVB exposures of 3.9 and 5.5% for the ISO and ANISO sky radiation distributions, respectively (Table 3) for all sky conditions. With the exception of clear sky conditions, the above differences in UVB exposure between the three cultivars lie within the range of the detectable error and are not statistically significant. The 13.2% exposure difference in clear sky conditions between York cv. and the other two cultivars is significant and merits further investigation in the future.

These differences in relative exposure between cultivars for different sky conditions indicated that the proportional exposure of the three cultivars over the course of the season depended on the proportion of diffuse and direct beam radiation and consequently on the proportion of clear sky versus cloudy days. A season with more clouds would result in an increased

Table 4
An example of calculated UVB exposures for 3 days from 2001: clear skies (July 11), hazy (August 8), and cloudy (June 21)

Cultivar	Model type	Sunny		Hazy		Cloudy	
		kJ m^{-2}	%	kJ m^{-2}	%	kJ m^{-2}	%
Bay	ISO	60.58	76.9	48.39	90.4	9.28	95.9
	ANISO	64.04	81.3	52.47	98.0	10.11	104.4
Williams 82	ISO	61.25	77.8	47.22	88.2	8.97	92.6
	ANISO	64.07	81.3	50.54	94.4	9.66	99.8
York	ISO	53.13	67.4	47.28	88.3	9.35	96.6
	ANISO	56.59	71.8	51.29	95.8	10.18	105.2
UVB total horizontal		78.77		53.51		9.68	
Diffuse fraction			53.8		86.6		99.9

All exposure data are in kJ m^{-2}. The total horizontal UVB exposures for all 3 days and diffuse fraction of these exposures are included, together with the percentage of the total horizontal UVB exposure for the ISO and ANISO data.

exposure on the top trifoliate of York cv. above that of Bay and Williams 82 cultivars. A season with fewer clouds would result in greater exposures of the Williams 82 and Bay cultivars above that of the York cultivar. A comparison between the overall exposures indicated that, in general, the Bay cultivar received a greater UVB exposure on the top trifoliate over the growing season than the Williams 82 or York cultivars, in large part due to the higher variation in heliotropic movement shown by the top trifoliate of the Bay cultivar in partly cloudy and clear skies.

The heliotropic response also has implications on the actual UVB exposure of soybean experiments using artificial UVB lamp enhancements. Typically, enhancements of UVB irradiance for UVB-effects studies are assumed to increase both diffuse and direct UVB proportionally. However, the enhancements are largely in the diffuse component of UVB, resulting in varying enhancements at the top trifoliate surface for each cultivar according to the cultivar's heliotropic leaf movements. A typical 30% enhancement of the horizontally measured diffuse UVB irradiance results in a 23% increase in UVB exposure on the top trifoliate of the Bay cultivar (seasonal exposure of 7.51 MJ m^{-2}) and 20% enhancements on both the Williams 82 (7.28 MJ m^{-2}) and York (7.28 MJ m^{-2}) cultivars above those of the measured total seasonal horizontal UVB exposure (6.06 MJ m^{-2}). This difference in exposure limits the ability to directly compare UVB effects between cultivars in the same season.

4. Conclusions

The heliotropic response is a means of mitigating UVB exposure and thus effects for soybeans. Bay cv. had the greatest overall variation in the heliotropic response of the three cultivars that resulted in the greatest exposure over the growing season to UVB under clear and hazy skies. York cv. showed less heliotropic movement than Bay or Williams 82 cultivars, and this was reflected in the lower UV exposure over the same time period. Although the Williams 82 cv. showed the greatest degree of heliotropic movement, it did not exceed the exposure of the Bay cv. for the 2001 growing season. This may be due to the earlier assumption that the leaf movement equations for Θ and α' did not change between clear and cloudy conditions. Therefore, a more detailed investigation of the leaf responses in cloudy conditions is needed to improve the exposure calculations for all weather conditions.

The absence of significant differences in the incidence angles between the field and greenhouse plants for all trifoliate leaves of the three cultivars indicated that the greenhouse environment did not inhibit the heliotropic response of the soybean plants. This signified that the greenhouse could provide a satisfactory environment for measuring soybean heliotropic movement if land was not available for field studies.

The modeled exposures of Williams 82, Bay and York cultivars demonstrated the differences between the UVB exposure obtained from assuming the leaves are horizontal compared with the leaf angle data obtained from field measurements of Θ and α'. The UVB exposures of all three cultivars were between 88 and 93% of the horizontal leaf exposure for an anisotropic sky radiation distribution and between 82 and 86% for the isotropic sky radiation distribution (Table 3). This result indicates that an assumption of horizontal soybean leaves in UVB exposure calculations can overestimate the exposure by up to 18%. The ambient exposures of the top trifoliate of three soybean cultivars differed substantially from that predicted from the horizontal exposure measurements and consequently plant responses to UVB should be related to the individual exposures and not to the horizontal exposure.

Results suggest that UV effects research may misclassify the sensitivity of cultivars to UVB radiation due to the variation in the ability of the cultivars to track the sun, and may mis-rank the sensitivity of cultivars as a result of the proportion of clear to cloudy skies at the research location. Additional work is needed to understand what proportion of the plant leaves is heliotropic and how the leaves orient under cloud cover.

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