Effect of Leaf Angle and Orientation on Photosynthesis and Water Relations in Silphium terebinthinaceum

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EFFECT OF LEAF ANGLE AND ORIENTATION ON PHOTOSYNTHESIS AND WATER RELATIONS IN SILPHIUM TEREBINTHINACEUM[1]

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ABSTRACT

Leaf angle and orientation were measured for 217 leaves from two populations of *Silphium terebinthinaceum* Jacq., a prairie forb with large, unlobed leaves. Seventy-five percent of leaves measured had an angle of deviation from horizontal of more than 60°, and 60% were oriented within 15° of North. Incident Photon Flux Density (PFD), leaf temperature, photosynthesis, stomatal conductance to CO_2, internal CO_2 concentration, transpiration, and water use efficiency (WUE) were measured on 67 pairs of leaves with the axes oriented in either a North–South (N–S) or East–West (E–W) direction. Leaves with axes oriented N–S intercepted higher levels of PFD during morning and afternoon and exhibited higher diurnal rates of photosynthesis and WUE. Leaf temperature was reduced in N–S leaves during midday as compared to E–W leaves, and was lower in vertical leaves than in those in a horizontal position. Therefore, it was concluded that leaf orientation and verticality enhance carbon gain and minimize water loss—characteristics which may have adaptive significance in a hot, stressful prairie environment.

SILPHIUM TEREBINTHINACEUM Jacq. (Asteraceae) is a forb which occurs throughout the prairies of Illinois (Mohlenbrock and Voigt, 1985). It is a deep-rooted perennial with large, unlobed leaves (up to 1 m long and 0.5 m wide) which begin growth in early spring and form a basal rosette which is often greater than 1 m in diameter (Gleason and Cronquist, 1963). A leafless stem emerges from the rosette in June/July and can attain a height of 4 m before reaching maturity and producing flowers in August and September.

The leaves of *S. terebinthinaceum* emerge from the basal rosette at a steep angle with axes that appear to orient in a North–South (N–S) position—laminae facing East–West (E–W) (personal observation). The adaptive value of vertical leaf angle and leaf orientation has been demonstrated for a number of species with small or deeply lobed leaves (Medina, Sobrado, and Herrera, 1978; Powells and Björkman, 1981; Nobel, 1980; Werk and Ehleringer, 1984, 1985, 1986). However, the potential benefit of such leaf characteristics to *S. terebinthinaceum* should be greater than for any plant previously

reported because of its extremely large, unlobed leaves (Vogel, 1970; Parkhurst and Loucks, 1972; Gates, 1980), active growth during the hottest months of summer (Mohlenbrock and Voigt, 1985), and the high temperatures, drought, and intense insolation of its prairie habitat (Weaver and Fitzpatrick, 1934; Risser et al., 1981).

A closely related prairie species with large, lobed leaves (up to 0.5 m long), *Silphium laciniatum,* produces vertical leaves that orient with the axes N–S (C. E. Martin, unpublished data). Martin observed that while leaf verticality did not appear to affect leaf temperature, N–S orientation increased light interception during early morning and late afternoon when temperatures were low, potentially maximizing photosynthesis and minimizing water loss.

It is the purpose of the present study to quantify the extent of verticality and orientation of leaves of *S. terebinthinaceum* and to determine the effect of these characteristics on leaf temperature, gas exchange (assimilation, A; transpiration, E; stomatal conductance, g_c; and internal CO_2 concentration, c_i) and Water-Use-Efficiency (WUE).

MATERIAL AND METHODS—All measurements were made on randomly sampled plants of *S. terebinthinaceum* from two populations in Madison County, IL: the Gordon Moore prairie, 1.5 km E of Alton on Illinois State Highway 140; and the Southern Illinois University experimental prairie at Edwardsville.

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TABLE 1. *Stomatal length, width, and density for adaxial and abaxial surfaces of leaves of* Silphium terebinthinaceum

Stomatal characteristic	Adaxial		Abaxial	
	$\bar{x}$ (SD)	N	$\bar{x}$ (SD)	N
Density cm⁻²	10,356 (2,471)	30	16,312 (3,677)	30*
Length μm	36.0 (4.3)	150	37.3 (4.3)	150*
Width μm	28.5 (3.0)	150	29.1 (3.3)	150

* $P < 0.05$.

Plants, and the leaves on each plant, were numbered and samples were chosen using a random number generator (TI-35 Plus, Texas Instruments). Data were collected on 22–24, 29, and 31 July and 2 August, 1988. All statistical tests were performed using SPSSX (Chicago, IL) and in the case of significant differences, $P < 0.05$ unless otherwise indicated.

Stomatal size, number, and distribution—Stomatal length, width and density were measured with an ocular micrometer on a Wild microscope Model M20 from nail polish leaf impressions obtained from leaves in the field (Hilu and Randall, 1984). Measurements were made of 5 stomata from each of 5 fields-of-view at 400× from both surfaces of one leaf from each of six plants ($N = 30$ for density; $N = 150$ for stomatal size). Leaf surfaces could be differentiated because the abaxial side had a prominent midrib and contained noticeably fewer stiff trichomes than the adaxial surface. It was noted that the adaxial side grew facing the center of the rosette and was thus shaded either by itself and the peduncle or by leaves on the opposite side of the rosette. This resulted in the abaxial surface intercepting more direct solar insolation in N–S leaves during both morning and afternoon (personal observation). Differences in mean stomatal size and number on abaxial and adaxial leaf surfaces were determined by analysis of variance (ANOVA) (Sokal and Rohlf, 1981).

Solar and incident Photon Flux Density—Photon Flux Density (PFD) was measured hourly from 0800 to 2000 hr on 31 July using a LI-COR 185-B light meter and LI-190SB quantum sensor. All PFD values are expressed as μmol m⁻² sec⁻¹. Incident PFD was measured on N–S and E–W oriented leaves ($N = 134$) with a LI-190SB sensor attached to the gas exchange system with the surface at a 90° angle with the ground. Significant difference was determined by the same procedure as in the gas exchange data (see *Gas exchange* section). All photosynthesis and PFD measurements were made on the side of the leaf receiving the highest incident PFD.

Leaf size, angle, and orientation—Leaf height and width were measured with a meter stick; leaf angle (the number of degrees the leaf petiole deviated from horizontal) with a protractor and plumb line; and leaf orientation (deviation of the leaf axis from N) with a handheld compass ($N = 217$ for all measurements). Leaf angle values were grouped into 8 classes (90, 80, 70, 60, 50, 40, 30, and ≤20°) and leaf orientation values into 6 classes of 15° each, and both sets of data compared to a uniform distribution by χ^2 (Sokal and Rohlf, 1981; Werk and Ehleringer, 1984).

Leaf temperatures—From 1200 to 1400 hr on 31 July leaf surface temperature was measured on 16 leaves held in a horizontal position and on 16 in a vertical position. Temperatures were measured with the thermocouple sensor which is mounted in the chamber of the photosynthesis system (see *Gas exchange* section). Five minutes after the leaf was clamped into the chamber, with the sensor surface in contact with the lamina which received the most solar radiation, leaf temperature was recorded. The data were tested for significant difference by ANOVA (Sokal and Rohlf, 1981).

Leaf surface temperature was recorded for 67 pairs of N–S and E–W oriented leaves during photosynthesis measurements (see *Gas exchange* section). The thermocouple sensor was in contact with the leaf surface which intercepted the most insolation, and would therefore be representative of the maximum leaf temperature at any given time.

Gas exchange—On four clear days (22–24 July and 2 August), A and E were measured on 67 pairs of leaves held in either a N–S or E–W position using a LI-COR 6200 Portable Photosynthesis System calibrated every three hours. The values for c_i and g_c were calculated using the equations of von Caemmerer and Farquhar (1981). A 0.25-L chamber was used and care was taken to avoid shading the leaf when inserting it into the leaf chamber. Measurements were taken within 4.2 ± 0.9 sec after insertion of the leaf into the chamber.

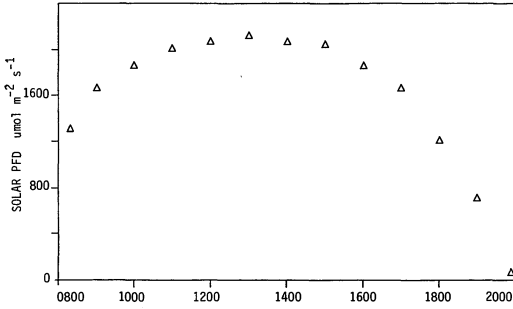On 21 July 1988, a preliminary experiment

Fig. 1. Solar PFD measured hourly from 0800 to 2000 hr (Central Daylight Time) on 31 July 1988. Solar angle is greatest (68°) at 1300 hr.
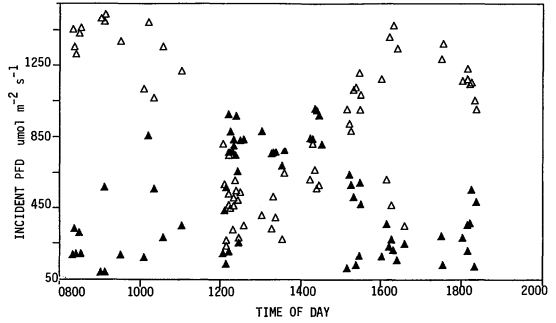

Fig. 2. Incident PFD measured on 67 pairs of leaves of *Silphium terebinthinaceum* on 22–24 July and 2 August, 1988. △ leaves with axes oriented in a N–S direction; ▲ leaves with axes oriented in an E–W direction.

was conducted on 42 leaves in full sunlight to determine the effect of relative humidity (RH) and vapor pressure deficit (VPD) on photosynthesis. The incoming air stream was passed through an external desiccant to achieve a range of chamber humidities from 22–71% and VPD from 1.6–4.3 kPa. There was no apparent effect of either RH or VPD on photosynthetic rate (data not shown). All gas exchange data reported in this study were measured when chamber RH was between 45 and 65% and VPD between 0.5 and 3.6 kPa.

All gas exchange data were tested by 2-way ANOVA for paired comparisons (Sokal and Rohlf, 1981). An arcsine transformation was performed on WUE data (Sokal and Rohlf, 1981). Tukey's HSD for post hoc comparisons was used to test means for differences in morning (0830–1200 hr), midday (1200–1400 hr), and afternoon (1400–1830 hr) values (Sokal and Rohlf, 1981).

RESULTS—Stomatal density was significantly greater on the abaxial leaf surface than on the adaxial surface. In addition, stomatal length, but not width, was significantly greater on the abaxial surface (Table 1).

Solar PFD reached a maximum intensity of 2,000 μmol m^{-2} sec^{-1} at ca. 1300 hr and declined to 50 μmol m^{-2} sec^{-1} at 2000 hr (Fig. 1). N–S leaves intercepted significantly more PFD during the morning (1,363, SD = 149) and afternoon (1,064, SD = 275) than E–W leaves (303, SD = 115; 312, SD = 169). However, during midday E–W leaves intercepted significantly more PFD than N–S leaves (715, SD = 246; 503, SD = 166) (Fig. 2; Table 2).

Mean leaf length was 81.6 cm (SD = 15.4). There was a significant deviation from randomness in both leaf angle and orientation. Seventy-five percent of the leaves measured had an angle of deviation from horizontal of more than 60°, and 60% were oriented within 15° of North (Fig. 3, 4).

Mean leaf temperature was significantly higher for leaves held in a horizontal position (37.7 C SD = 2.8) during midday as compared to those held vertically (34.0 C SD = 2.7) (Table 2). Leaves of N–S oriented leaves had significantly higher surface temperatures during both morning and afternoon ($P < 0.01$), but not during midday (Table 2).

TABLE 2. *Leaf temperature and incident PFD measured on 67 pairs of leaves of* Silphium terebinthinaceum *on 22–24 July and 2 August 1988, and surface temperature of 16 vertical (V) and 16 horizontal (H) leaves on 31 July 1988.*[a] *AM (0800–1200); midday (1200–1400); and PM (1400–1830)*

		Time			
		AM	Midday	PM	Diurnal
Parameter	Orient.	$\bar{x}$ (SD)	$\bar{x}$ (SD)	$\bar{x}$ (SD)	$\bar{x}$ (SD)
Leaf temp (C)	N–S	30.7 (2.0)*	36.0 (3.1)	32.9 (1.7)**	33.8 (3.2)**
	E–W	28.7 (2.1)	35.9 (2.9)	31.3 (2.4)	32.7 (3.9)
	V	—	34.0 (2.7)**	—	—
	H	—	37.7 (2.8)	—	—
PFD (μmol m^{-2} sec^{-1})	N–S	1,363 (149)***	503 (166)***	1,064 (275)***	884 (408)***
	E–W	303 (115)	715 (246)	312 (169)	485 (293)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. — Indicates time period when no measurements were made.
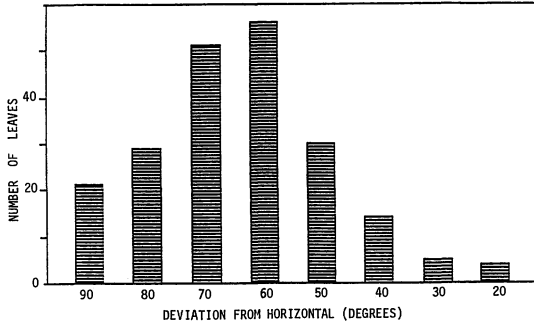[a] Central Daylight Time.

Fig. 3. Leaf angle (measured as the number of degrees the leaf petiole deviated from horizontal) of 217 leaves of *Silphium terebinthinaceum*.
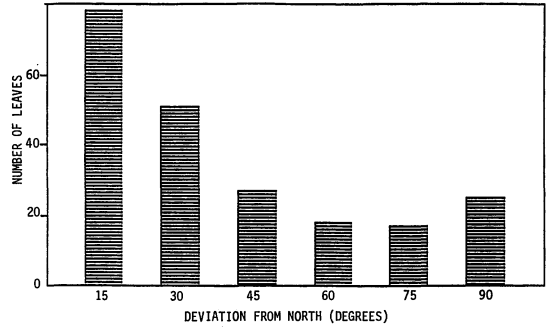

Fig. 4. Leaf orientation (measured as the deviation of the leaf axis from N) of 217 leaves of *Silphium terebinthinaceum*.

Mean values and standard deviations for A, g_c, c_i, E, and WUE are shown in Table 3. A, c_i, and WUE were significantly higher in N–S oriented leaves compared to E–W leaves during the morning ($P < 0.001$; $P < 0.01$; $P < 0.05$) and afternoon ($P < 0.01$; $P < 0.001$; $P < 0.05$). E was significantly higher for N–S leaves during the morning ($P < 0.01$), but not during midday or in the afternoon. The value g_c was not significantly different between the two groups for any of the above values at any time of day. Daily fluctuations for A, g_c, and c_i are shown in Fig. 5–7; for E and WUE, Fig. 8, 9.

DISCUSSION—Data collected from two populations of *Silphium terebinthinaceum* clearly indicate that leaf angle and orientation are non-random. Leaves exhibited a significant preference for N–S orientation, with the abaxial laminae toward the sun, and for leaf angles of less than 30° from vertical. In fact, the degree

of verticality reported for leaves of plants in this study is probably less than would have been measured earlier in the growing season when the plant rosettes were smaller. As the rosettes enlarge, old leaves are forced outward from the emerging peduncle which tends to increase the angle of deviation from vertical (personal observation).

These morphological features maximize interception of PFD during morning and afternoon periods when ambient temperature is low. In addition, leaf temperature is minimized during the midday period when solar insolation and ambient temperature are usually high. The data reported for temperatures of vertical versus horizontal leaves indicate that leaf verticality results in a significant reduction in heat load. Similar patterns have also been observed in other species from various habitats (Gibbs and Patten, 1970; Medina et al., 1978; Shaver, 1978; Nobel, 1980; Werk and Ehleringer, 1984). However, because of its unusually large, un-

TABLE 3. *Gas exchange characteristics for 67 pairs of leaves of* Silphium terebinthinaceum *measured on 22–24 July and 2 August 1988.*[a] *AM (0800–1200); midday (1200–1400); PM (1400–1830)*

		Time			
		AM	Midday	PM	Diurnal
Parameter	Orient.	$\bar{x}$ (SD)	$\bar{x}$ (SD)	$\bar{x}$ (SD)	$\bar{x}$ (SD)
A (μmol CO_2 m^{-2} sec^{-1})	N–S	9.7 (2.3)***	6.7 (1.7)	6.7 (2.3)**	7.4 (2.3)***
	E–W	4.9 (2.1)	7.2 (1.8)	4.8 (1.6)	5.9 (2.1)
g_c (mol m^{-2} sec^{-1})	N–S	0.3 (0.1)	0.3 (0.1)	0.2 (0.1)	0.3 (0.1)
	E–W	0.3 (0.1)	0.3 (0.1)	0.2 (0.1)	0.3 (0.1)
c_i (PPM)	N–S	153.6 (32.4)**	230.0 (35.8)	173.0 (40.0)***	193.6 (48.8)***
	E–W	221.5 (44.9)	225.5 (36.9)	216.8 (36.0)	221.5 (38.0)
E (mmol H_2O m^{-2} sec^{-1})	N–S	3.2 (0.6)**	4.3 (1.1)	2.9 (1.0)	3.6 (1.1)*
	E–W	2.7 (0.6)	4.2 (1.0)	2.7 (1.0)	3.4 (1.2)
WUE (A/E)	N–S	3.1 (0.8)*	1.6 (0.5)	2.4 (0.7)*	2.2 (0.9)**
	E–W	2.0 (0.9)	1.7 (0.4)	1.9 (0.6)	1.8 (0.6)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
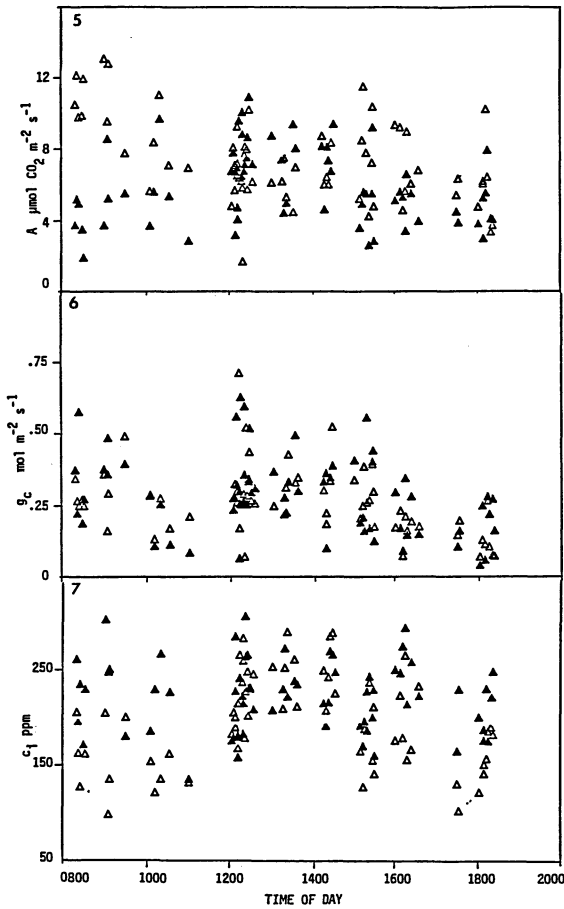[a] Central Daylight Time.

Fig. 5–7.   5. A, 6. g_c, 7. c_i of 67 pairs of leaves of *Silphium terebinthinaceum* on 22–24 July and 2 August 1988. △ leaves with axes oriented in a N–S direction; ▲ leaves with axes oriented in an E–W direction.

Fig. 8, 9.   8. E, 9. WUE of 67 pairs of leaves of *Silphium terebinthinaceum* on 22–24 July and 2 August 1988. △ leaves with axes oriented in a N–S direction; ▲ leaves with axes oriented in an E–W direction.

lobed leaves, *S. terebinthinaceum* may benefit from these leaf characteristics more than any plant studied thus far (Vogel, 1970; Parkhurst and Loucks, 1972; Gates, 1980). Additionally, the exposure to the sun of the abaxial laminae, which have larger stomata and greater stomatal density, may stimulate a rapid stomatal response to light and maximize early morning photosynthesis (Zeiger, Field, and Mooney, 1981).

Leaves which oriented N–S had significantly higher A in both morning and afternoon, resulting in higher A over an entire diurnal period. This appears to be primarily a function of higher levels of incident PFD. During the midday period, E–W leaves intercepted significantly more PFD, but, perhaps due to high temperatures and subsequent increase in E, failed to demonstrate significantly higher rates of A. This phenomenon has been reported in other species (Sharkey, 1984; Bunce, 1988).
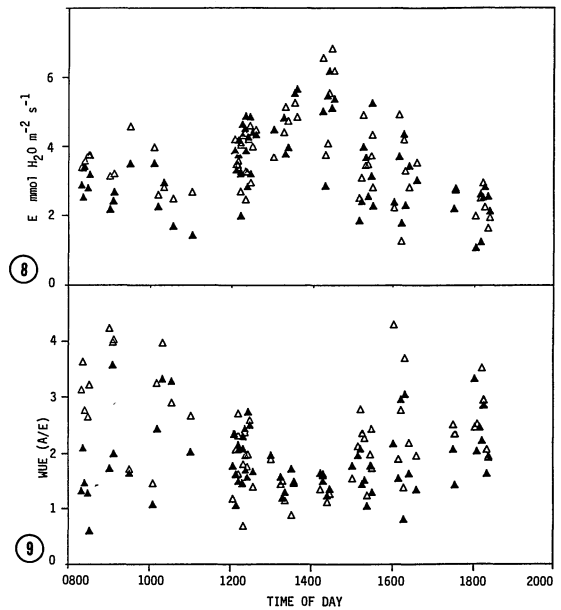
The only gas exchange parameter which did not differ significantly between N–S and E–W oriented leaves was g_c. Therefore, it would appear that photosynthesis was not limited by the stomata, but by other factors (Boyer, 1965; Farquhar and Sharkey, 1982; Sharkey, 1984; Bunce, 1988). An examination of the c_i data supports this assumption: c_i is significantly higher in E–W leaves during both morning and afternoon, in spite of the fact that g_c is not significantly higher. This is an indication that some metabolic factor is limiting photosynthesis in E–W leaves during these time periods (Wong, Cowan, and Farquhar, 1979, 1985).

N–S oriented leaves had higher rates of E during the morning which resulted in a higher diurnal water loss. However, the higher rate of A in N–S leaves with respect to those oriented E–W resulted in their maintaining a higher diurnal WUE. In many plant species for which the acquisition of water is problematic, a high WUE is considered an essential adaptive feature (Cowan and Farquhar, 1977; Cowan, 1982; Forseth and Ehleringer, 1982). *Silphium terebinthinaceum,* however, has roots that penetrate the water table (Mohlenbrock and Voigt, 1985) and in this study exhibited no overt signs of water stress throughout the progressively dry summer. Similarly, Weaver and Fitzpatrick (1934) reported that *S. terebinthinaceum* appeared unaffected by the extreme drought of

1933–1934. In view of these observations, it is not immediately clear what adaptive advantage is conferred by a high WUE.

In summary, *Silphium terebinthinaceum* exhibited nonrandom leaf orientation and angle. An increase in intercepted PFD during morning and afternoon periods by N–S oriented leaves resulted in higher rates of A and WUE relative to leaves oriented in an E–W direction. In addition, leaf temperatures were reduced during periods of high insolation and ambient air temperature. Although the adaptive value of high WUE is not clear for *S. terebinthinaceum*, the maintenance of lower leaf temperatures and higher A in vertical leaves which orient N–S may be critical to survival in the hot, stressful prairie environment.

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