INTRODUCTION

Canopy architecture strongly affects a plant's capability to intercept solar radiation. This is because canopy architecture is the geometrical property and spatial arrangement of the plant's individual foliage elements (Ross 1981), and it includes properties such as leaf area, leaf inclination (angle from zenith), leaf azimuth (angle from North in a clockwise direction) and leaf shape. Of these properties, the effect of leaf area and orientation (leaf inclination and azimuth) on solar radiation interception is most well understood. Their effect on solar radiation interception can also be mathematically described using Beer's law as shown by Monsi and Saeki (1953), and Ross (1981).

The effect of leaf shape, however, on solar radiation interception is little known. Its relationship with solar radiation interception is also not directly accounted for in Beer's law. All plant properties being equal, it is unclear how leaves having a given shape would collectively affect the solar radiation regime within the plant stand and thus the total solar radiation interception. Leaves with lobes, for example, are thought to reduce self-shading and to produce deeper sunflecks within a canopy (Horn 1971). Computer simulations by Niklas (1989), however, revealed no change in the amount of daily solar radiation interception due to leaf lobbing per se. That the effect of leaf shape on solar radiation interception is unclear and little studied is not surprising. It is experimentally difficult to assess the effect of leaf shape on solar radiation interception because this factor cannot be isolated and studied independently from other plant or leaf factors (Niklas 1989). It is impossible, for example, to find real plants that are identical in all aspects apart for their leaf shapes. One solution is to use computer-generated plants. By controlling all plant and leaf aspects, it is possible to study the effect of leaf shape per se on solar radiation interception.

It is thus the objective of this study to evaluate the effect of various leaf shapes on both direct and diffuse solar radiation interception using a detailed solar radiation model. If the role of leaf shape on solar radiation interception is shown to be important, this could help to better design or select crop varieties that have the "proper leaf form" for optimum plant production. This study would also help to understand the role of leaf shape as a plant adaptation mechanism to adapt to certain environmental conditions or stresses by altering, among others, the amount of solar radiation being captured.

MATERIALS AND METHODS

3-D solar radiation model

The canopy space of a plant was divided into a network of 3-D cuboids that was perpendicular to the planting row direction. The height, width and length of the network were equal to the plant height, inter-row and intra-row planting distance,

respectively. In this study, the inter-row and intra-row planting distance were set at 0.6 and 0.3 m, respectively, and the planting row was in the North-South direction.

For each cuboid in the network, three kinds of information were required: a) leaf area density, b) leaf orientation distribution, or the G-function, and c) mean travelling distance of a solar beam. This information was required to calculate the probability $P_{dr, k}(r)$ of a single solar beam penetrating or exiting the k-th cuboid in the network:

$$P_{dr,k}(r) = \exp\left[-G_k(r) \cdot \rho_{f,k} \cdot s_k \cdot \sqrt{1-\sigma}\right] \cdot \prod_{c=1}^{k-1} \exp\left[-G_c(r) \cdot \rho_{f,c} \cdot s_c \cdot \sqrt{1-\sigma}\right]$$
(1)

where the multiplicative series c=1 to (k-1) represents every cuboid visited sequentially by the beam in reaching the target cuboid k; $G_c(r)$ is the G-function in the c-th cuboid; $\rho_{f,c}$ is the leaf area density in the c-th cuboid; s_c is the beam path length in the c-th cuboid; and σ is the leaf scatter coefficient, taken as 0.2 (Tournebize & Sinoquet 1995). The so-called G-function G(r) is regarded as the average projection per unit foliage area in the sun direction r, (Ross, 1981), where the sun direction r is described by solar inclination θ and azimuth ϕ . The $G_c(r)$ or $G_c(\theta, \phi)$ in the c-th cuboid is calculated by

$$G_c(\theta, \phi) = \sum_{j=1}^{N} L_{c,j} \left| \cos \theta \cos \theta_L + \sin \theta \sin \theta_L \cos \left(\phi - \phi_L \right) \right|_{c,j} / \sum_{j=1}^{N} L_{c,j}$$
 (2)

where $L_{c,j}$ is area of the *j*-th leaf in the *c*-th cuboid; *N* is total number of leaves in *c*-th cuboid; and θ_L and ϕ_L are the leaf normal inclination and leaf normal azimuth of the *j*-th leaf in the *c*-th cuboid, respectively. (Thanisawanyangkura et al. 1997). Calculations for s_c were based on simple geometry as described by Gijzen and Goudriaan (1989), and Sinoquet and Bonhomme (1992).

In this study, a simulation run would begin by "pushing" a total of four equally-spaced beams (coming from solar direction r) into each cuboid in the uppermost level of the network. The traversal of each of these beams down the network was simulated using ray-tracing principles (Gijzen & Goudriaan 1989; Sinoquet & Bonhomme 1992). And for every cuboid that could be reached by a given beam direction, Eq. (1) was used to calculate the beam's penetration probability. This information was then stored. These steps were repeated for the traversal of the next beam "pushed" into the network. Consequently, at the end of a simulation run, the mean penetration probability for every cuboid in the network could be determined.

The total fraction of direct solar radiation intercepted F_{dr} was calculated by

$$F_{dr} = 1 - \overline{P_{dr,k=ground}(r)} \tag{3}$$

where $\overline{P_{dr,k=ground}(r)}$ is the average direct beam penetration probability for all cuboids on the ground level only (i.e., the overall mean probability of a direct solar beam to reach the soil surface).

Unlike direct solar radiation, diffuse solar radiation does not come from a single direction but uniformly from all directions. The penetration probability of diffuse solar radiation $P_{df, k}$ in the k-th cuboid is approximated by summing the penetration probability of direct beams over the whole sky at three and four solar inclination θ and azimuth ϕ angles, respectively (θ = 15°, 30° and 75°, and ϕ = 45°, 135°, 225° and 315°), and taking the mean of the 12 values (de Castro and Fetcher, 1998), or

$$P_{df,k} = \frac{1}{12} \sum_{r} P_{dr,k}(r) = \frac{1}{12} \sum_{\theta} \sum_{\phi} P_{dr,k}(\theta,\phi)$$
 (4)

The total fraction of diffuse solar radiation intercepted F_{df} was calculated by

$$F_{df} = 1 - \overline{P_{df,k=ground}} \tag{5}$$

where $\overline{P_{df,k=ground}}$ is the average diffuse beam penetration probability for all cuboids on the ground level only.

Finally, simulations of hourly solar radiation interception were done from 8:00 to 18:00 local hour, for the year 2003, day of year 152, and for Serdang site, with latitude and longitude of 3.24° N and 101.47° E, respectively.

3-D plant geometry

Located at the centre of the 3-D network of cuboids was a computer-generated plant (prototype) where, in this study, its leaf number, leaf azimuth, leaf position, planting distance, and plant height were held constant. Only its leaf shape, area and inclination were varied. Six simple shaped leaves were selected in this study to assess their effect on solar radiation interception: round (RD), square (SQ), triangle (TR), inverted triangle (ITR), ellipse (EL) and lobe (LB) (Figure 1). The effect of these leaf shapes on solar radiation interception was examined in the following three conditions: a) leaf area index (LAI) 0.5, 1.0 and 3.0; b) leaf inclination 22.5°, 45° and 90°; and c) leaves with and without petioles.

In all of the above conditions, total plant height was set at 1.0 m, and the number of leaves per plant was set at 12 where the leaves were arranged in a whorled phyllotaxy with three leaves or leaflets per node. Therefore every three leaves were positioned at four different plant heights (1.0, 0.7, 0.4 and 0.1 m), and for each height, the azimuth of the three leaves were separated from each other by 120°. The azimuths of the three leaves positioned at plant height 1.0 and 0.4 m were

 0° , 120° and 240° , respectively, and the azimuths of three leaves positioned at plant height 0.7 and 0.1 m were 60° , 180° and 300° , respectively.

The area of every leaf in a plant was set equal to each other. Area per leaf was calculated by taking into account the leaf shape, number of leaves, planting distance and LAI. For example, given 12 leaves per plant, LAI 1.0 and planting distance of 0.6x0.3 m, the area and dimension (width by length) of every square leaf (SQ) per plant would be 0.0150 m² and 0.1225 by 0.1225 m, respectively. Note that the leaf shapes for prototypes SQ, TR and ITR were set as equilateral; that is, for a given shape, all its sides are equal (Figure 1). For the EL prototype, the length of its elliptic leaf shape was set approximately double the leaf length of SQ prototype, and the widest leaf width for the EL occurred at half the leaf length. The length of the lobed leaves, LB, was set approximately equal to the leaf length of SQ prototype, and the length of the three equally-spaced lobes was set as half the total leaf length LB.

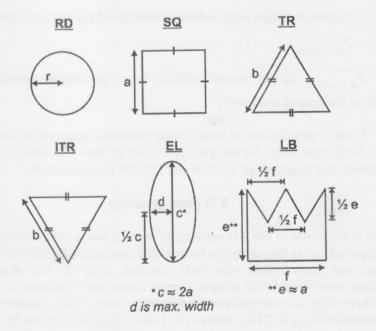


Figure 1. Leaf shapes for the six plant prototypes: round (RD), square (SQ), triangle (TR), inverted triangle (ITR), ellipse (EL) and lobe (LB).

One of the properties required by Eq. (1) is the leaf area density within a cuboid. Because a leaf may not lie entirely within a cuboid, the leaves were described as 3-D polygons so that the Sutherland-Hodgman's 3-D polygon clipping algorithm (Sutherland & Hodgman 1974) could be used to determine the section of a leaf polygon encompassed by a given cuboid. Applying this algorithm to all the leaves of the plant would give the total leaf area encompassed within any cuboid.

Leaf area density was calculated by dividing the enclosed leaf area by the cuboid volume.

Statistical analysis

Analysis of variance (ANOVA) was not performed in this study because this was a simulation study where there were no replicates. The plants used were all computergenerated to obtain plants that were exact in all aspects except for their leaf shapes. In reality, such plants do not exist.

RESULTS AND DISCUSSION

As expected, the mean hourly interception of solar radiation was effected by the leaf inclination and LAI (Table 1), where the interception of both direct and diffuse solar radiation increased with increasing LAI and leaf inclination (i.e. increasingly larger and more horizontally inclined leaves).

Most importantly, however, given a leaf inclination and LAI, the mean hourly interception of solar radiation was effected by the leaf shape, albeit to a rather small extent (Table 1). The differences in solar radiation interception among the six plant prototypes were not more than 11% from each other. Moreover, their differences declined to not more than 5% from each other for full or near canopy cover (i.e., LAI 3.0). At near or full canopy cover, the total fraction of direct or diffuse solar radiation intercepted was at near maximum 1.0; consequently, any further advantages of having a particular leaf shape to increase solar radiation interception at this stage would be small. As shown in Table 1, the mean hourly interception of both direct and diffuse solar radiation by the plant prototypes can be distinguished into two groups, where solar radiation interception decreased in the following manner: (ITR ≈ EL) > (RD ≈ SQ ≈ TR ≈ LB). RD, SQ and TR leaf shapes did not show any differences among them in their solar radiation interception. Lobed leaves (LB) are often thought to alter the plant-radiation regime significantly by producing deeper sunflecks within the canopy (Horn 1971). Nonetheless this study showed no effect of leaf lobbing per se (LB prototype) on solar radiation interception, as also reported by Niklas (1989). In his simulation study, the gaps between the leaf lobes of the short ragweed (Ambrosia artemisiifolia L.) were approximately 45% of the leaf area, and the gaps were numerous with each gap small and shallow. But in this study the gaps between the lobes for the LB prototype were approximately 30% of the leaf area, and these gaps were few with each gap wide and deep. Despite these differences in both these studies, leaf lobbing has so far been shown not to affect solar radiation interception.

The interception of both direct and diffuse solar radiation for all prototypes could however be further increased by the presence of leaf petioles (Table 2). Compared to sessile (non-petiole) leaves, leaves with petioles (100 mm in length) further increased the solar radiation interception by not more than 12%, but this increase generally declined for full or near canopy cover. The increase in solar radiation interception due to the presence of petioles was generally most

pronounced for RD, SQ, TR and LB plant prototypes (an average gain of 7%) as compared to ITR and EL prototypes (an average gain of 3%) (Table 2). This difference is because, as shown earlier, ITR and EL prototypes intercepted the most fraction of direct and diffuse solar radiation as compared to other plant prototypes. Thus, additional advantages of having leaf petioles to further increase solar radiation interception would be small for the EL and ITR prototypes.

Table 1. Mean hourly fraction of intercepted solar radiation for all plant prototypes with sessile (non-petiole) leaves. Note: in the same table column, values in the brackets indicate the difference (in percent) from the fraction of solar radiation intercepted by the RD prototype.

(a) Direct solar radiation

Proto-		LAI	0.5	nal ben		LAI 1				LAI 3				
type	22.5°	45°	90°	Mean	22.5°	45°	90°	Mean	22.5°	45°	90°	Mean		
RD	0.258	0.278	0.279	0.272 (0.0)	0.401 (0.0)	0.458	0.472 (0.0)	0.443	0.722 (0.0)	0.812	0.848	0.794 (0.0)		
SQ	0.267 (3.4)	0.283	0.281 (0.8)	0.277 (2.0)	0.407	0.464 (1.3)	0.473 (0.1)	0.448 (0.9)	0.729 (0.9)	0.816 (0.4)	0.849 (0.1)			
TR	0.261 (1.1)	0.280 (0.9)	0.275	0.2.2	0.415 (3.6)		0.469 (-0.7)		0.731 (1.3)		0.842 (-0.6)			
ITR	0.279 (8.2)	0.306 (10.2)		0.295 (8.6)	0.440 (9.8)	0.498	0.505 (7.0)	0.481 (8.5)	0.751 (4.0)	0.00	0.876			
EL	0.275 (6.3)	0.307 (10.6)	0.305	0.295 (8.6)	0.442 (10.2)	10 11	0.508	0.482 (8.7)	0.750 (3.9)	0.833 (2.6)	0.878 (3.6)	0.820 (3.3)		
LB	0.264 (2.3)	0.280 (0.8)	0.258	0.267 (-1.5)	0.417 (4.2)	0.462 (1.0)	0.456 (-3.5)	0.445 (0.4)	0.734 (1.7)	0.812 (0.0)	0.839	10 11		

(b) Diffuse solar radiation

Proto-		LAI	0.5	aber .		LAI 0.5 LAI 1						LAI 3			
type	22.5°	45°	90°	Mean	22.5°	45°	90°	Mean	22.5°	45°	90°	Mean			
RD	0.283	0.293	0.303	0.293	0.438	0.482	0.509	0.476 (0.0)	0.726 (0.0)		0.874 (0.0)	0.804 (0.0)			
SQ	0.291 (3.0)	0.300 (2.5)	0.305	0.299 (2.1)	0.445 (1.7)	0.486 (0.8)	0.511 (0.3)	0.481 (0.9)		0.814 (0.1)	0.874 (0.0)	0.796 (-1.1)			
TR	0	0.300 (2.5)	0.298	0.298			0.509 (-0.1)				0.867 (-0.8)				
ITR	0.295 (4.5)	0.02.	0.326		0.472 (7.9)		0.538 (5.7)		0.758 (4.3)		0.907 (3.8)	0.837 (4.0)			
EL	0.303 (7.3)	0.325 (10.8)	0.001	0.319 (9.1)	0.476 (8.8)		0.546 (7.3)	0.514 (7.9)	0.753 (3.7)	0.851 (4.7)	0.908 (4.0)	0.838 (4.2)			
LB	0.294 (4.1)	0.301 (2.9)		0.292 (-0.3)	0.462 (5.5)		0.493 (-3.2)		0.742 (2.1)		0.863				

Interestingly, stretching a leaf longer and narrower while maintaining the same leaf area augmented solar radiation interception (Figures 2 and 3). The elliptic, sessile leaves for the EL prototype were stretched longer by 100 mm while maintaining the same leaf area. And compared to the non-modified EL leaves, the longer and narrower EL leaves further increased the interception of both direct and diffuse solar radiation by not more than 14%. This increase in interception, like the previous scenarios, declined for full or near canopy cover.

Table 2. Mean hourly fraction of intercepted solar radiation for all plant prototypes with petiole leaves. Note: the values in the brackets indicate the difference (in percent) between the fraction of solar radiation intercepted by sessile (non-petiole) and petiole leaves of the same prototype, LAI and leaf inclination (i.e. compare with Table 1).

(a) Direct solar radiation

Proto-		LA	I 0.5			LA	I 1		LAI3				
type	22.5°	45°	90°	Mean	22.5°	45°	90°	Mean	22.5°	45°	90°	Mean	
RD	0.283	0.302 (8.6)	0.291 (4.5)	0.292 (7.5)			0.488			0.826			
SQ			0.302 (7.5)				0.501 (6.1)			0.839 (2.8)			
TR			0.306 (11.0)				0.507 (8.2)			0.838			
ITR			0.303 (1.3)				0.513 (1.5)	0		0.849			
EL		0.316 (2.9)		0.309 (4.6)		390.00	0.524 (3.0)			0.835			
LB	0.289 (9.2)	0.312 (11.3)	0.284 (9.9)	0.295 (10.1)	0.456 (9.2)	0.502 (8.6)	0.482 (5.8)	0.480 (7.8)	0.750 (2.2)	0.838	0.872 (4.0)	0.820 (3.2)	

(b) Diffuse solar radiation

Proto-	2 221115 ()	LAI 0.5				LAI 1				LAI 3			
type	22.5°	45°	90°	Mean	22.5°	45°	90°	Mean	22.5°	45°	90°	Mean	
RD	0.315	0.319	0.318	0.317	0.477	0.512	0.531	0.507	0.750	0.842	0.905	0.832	
	(11.5)	(8.8)	(4.8)	(8.3)	(9.0)	(6.1)	(4.2)	(6.3)	(3.3)	(3.6)	(3.6)	(3.5)	
SQ	0.321	0.328	0.329	0.326	0.485	0.524	0.542	0.517	0.755	0.849	0.913	0.839	
	(10.2)	(9.4)	(7.6)	(9.1)	(9.0)	(7.7)	(6.2)	(7.6)	(7.9)	(4.4)	(4.4)	(5.4)	
TR	0.322	0.332	0.331	0.328	0.492	0.530	0.547	0.523	0.755	0.847	0.910	0.837	
	(9.0)	(10.8)	(10.9)	(10.2)	(6.3)	(8.0)	(7.5)	(7.3)	(2.0)	(4.6)	(5.0)	(4.0)	
ITR	0.325	0.331	0.334	0.330	0.492	0.527	0.552	0.524	0.768	0.865	0.913	0.849	
	(10.3)	(2.1)	(2.5)	(4.8)	(4.2)	(1.2)	(2.6)	(2.6)	(1.4)	(2.3)	(0.7)	(1.5)	
EL	0.322	0.335	0.343	0.333	0.492	0.534	0.563	0.530	0.776	0.866	0.902	0.848	
	(6.1)	(3.3)	(3.8)	(4.4)	(3.4)	(2.6)	(3.0)	(3.0)	(3.0)	(1.7)	(-0.7)	(1.2)	
LB	0.323	0.333	0.305	0.321	0.495	0.530	0.519	0.515	0.755	0.847	0.903	0.835	
	(10.0)	(10.6)	(9.0)	(9.9)	(7.1)	(8.0)	(5.3)	(6.8)	(1.7)	(4.2)	(4.7)	(3.6)	

Coefficient of variation (c.v.) was calculated to determine the uniformity of spread of leaf area within the canopy. Recall that the canopy was divided into a network of 3-D cuboids where each cuboid has a certain value of leaf area. The c.v. was calculated then as

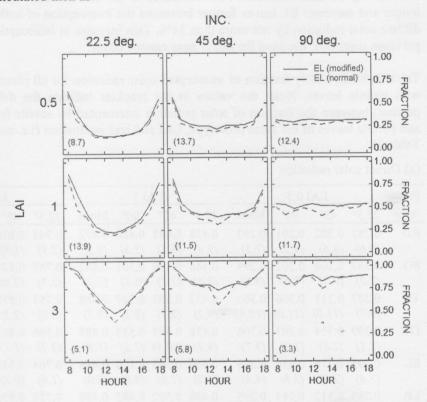


Figure 2. Comparisons between the fraction of intercepted direct solar radiation by the EL (modified) and EL (normal) prototypes. Note: values in brackets indicate the mean hourly difference (in percent) between the fraction of intercepted solar radiation by the EL (modified) and EL (normal) prototypes. LAI and INC are the leaf area index and solar inclination, respectively.

$$c.v. = 100 \, s/a \tag{6}$$

where s is the standard deviation of leaf area; and a is the mean leaf area in each cuboid. For every prototype, there was a strong negative correlation coefficient between the mean solar radiation intercepted and c.v. of leaf area (Figure 4). Because all plant properties were held constant in this study, a low c.v. value would indicate a more uniform spread or distribution of leaf area in the canopy aerial space. This in turn means lesser self-shading and clumping of leaves. This study also showed that although TR and ITR prototypes had both triangle leaves, ITR intercepted more solar radiation than TR because the orientation of ITR leaves was such that the bulk of the leaf area was away from the plant stem (i.e. leaves broader

properties being equal, grass species, maize and oil palm trees, due to their long, narrow leaves, would intercept more solar radiation than plants that have short, wide leaves. Leaves that are broader at the apex than at the basal would also increase solar radiation interception because this reduces the bunching or clustering of leaves near the plant stem, causing a more uniform spread of leaf area.

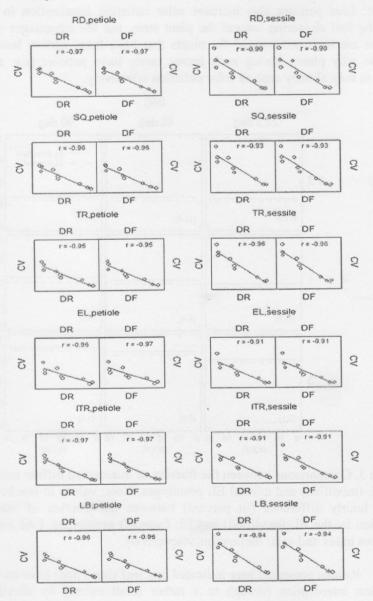


Figure 4. Relationship between the coefficient of variation of leaf area density (CV) and the fraction of intercepted direct (DR) and diffuse (DF) solar radiation for all the plant prototypes.

Finally, the differences in leaf shapes did not appear to affect the diurnal variation of direct solar radiation interception (Figure 5), where for each plant prototype, the interception of direct solar radiation depended on the solar position, whereby the solar radiation interception decreased gradually as the sun begun to align in parallel to the planting row direction (N-S) at 13:00 hours at this site.

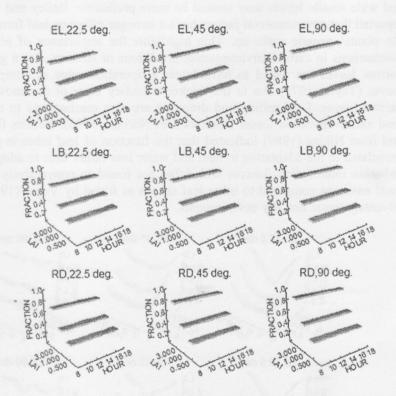


Figure 6. Diurnal fraction of intercepted diffuse solar radiation for the EL, LB and RD plant prototypes. Note: other plant prototypes showed similar diurnal variation.

Direct solar radiation interception decreased and was at the lowest at 13:00 hours, and after this hour solar radiation interception gradually increased. The effect of a pronounced planting row direction on solar radiation capture has often been observed (Wallace 1997). This effect arises because when the sun is parallel to the planting row direction the impediment by the canopies on solar beams is less as compared to that when the sun is non-parallel to the planting row direction. With increasing leaf inclination, the diurnal variation of direct solar radiation interception would decrease; that is, becoming more constant throughout the day. It is widely known that the interception of solar radiation by horizontal leaves is not affected by the solar position (Goudriaan & van Laar 1994). Unlike the diurnal variation in direct solar radiation interception, the diffuse solar radiation interception was constant throughout the day (no diurnal variation) (Figure 6) because diffuse solar radiation was considered in this study to radiate uniformly from all directions of the

The results here may indicate that crop yields could be increased, albeit slightly, by designing or selecting crop varieties that have longer and narrower leaves, leaves with longer petioles, or leaves that are broader at their apex than at their basal. Nonetheless, in stressed environments, having such leaves may be detrimental due to the heavy solar radiation load on them. In such conditions, short and wide sessile leaves may instead be more preferable. Bailey and Sinnott (1916) reported that environmental factors have a stronger effect on leaf form and size than the plants' genetic make-up. This highlights the importance of plant adaptation mechanisms in certain environmental conditions or stresses. For a given leaf area, narrow leaves are found to have lower evaporation rates as compared to broad leaves (Taylor 1975) due to the thicker boundary layer of non-moving air on the narrow leaves. Leaf rolling and drooping are also mechanisms to reduce thermal load and evaporation losses (Campbell & Norman 1998). Results from this study and from Niklas (1989) indicated that the function of leaf lobes is probably more associated to the adaptation to heat and water loss rather than to adaptation to solar radiation interception. Leaves with lobes are found to convectively dissipate heat most easily as compared to other leaf shapes as found by Vogel (1970), which are advantageous in hot, dry environments.

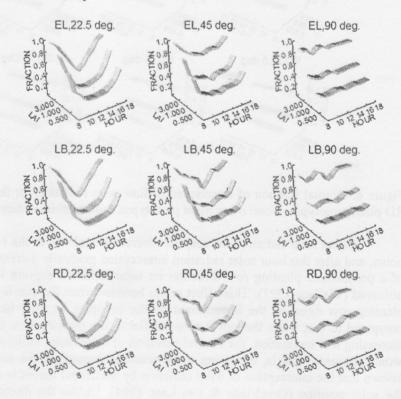


Figure 5. Diurnal fraction of intercepted direct solar radiation for the EL, LB and RD plant prototypes. Note: other plant prototypes showed similar diurnal variation.

whole sky; thus, the canopy architecture and solar position have no effect on the diurnal variation of the fraction of diffuse solar radiation intercepted (see also Figure 3).

CONCLUSION

Leaf shape was shown to have an effect on solar radiation interception, although its effect was to a rather small degree of not more than 11% increase in solar radiation interception. All plant properties being equal, solar radiation interception could be increased by having leaf shapes that are: 1) long and narrow, 2) broader at the apex than at the basal, and 3) supported by leaf petioles. Leaf shapes that increase solar radiation interception are those that cause the canopy to be spread out more uniformly or homogenously in the aerial space. This means that solar radiation interception can be increased by reducing leaf clustering and self-shading.

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