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The Relationship between Photosynthetic Active Radiation and Leaf Orientation

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光合成有効放射와 葉向과의 關係

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ABSTRACT

Photosynthetically Active Radiation(PAR) affects the growth of plants as well as their photosynthetic rates. A mathematical model for intercepted solar radiation on the tilted leaf with any azimuth angle was established and the leaf orientation in which receives the maximum solar radiation was determined each month, during the growing season, and for an year. PAR was maximized at the leaf elevation of 50°~60° in the winter, at that of 20°~40° in the spring and autumn, and at the horizontal in the summer. During the growing season the maximum value was at the elevation of 0°~20°, and for an year it was at 20°~40°. On the whole the leaves of tilt angle 0°~40° received much radiation comparing with those of other tilt angles.

The theoretical tendencies were compared with the distribution of leaf orientation measused practically. The average leaf elevation of maple tree was 17.0°±12.0°, and that of ginkgo was 29.8°±16.0°. Several results from other literatures support our suggestion that cumulative effect of the relationships between surface normal vector and a vector pointing in the direction of the radiation determine the leaf orientation.

INTRODUCTION

Leaves orient themselves in response to light or gravity. The orientation of the leaves of higher plants with respect to the sun plays an important role in the regulation of the amount of photosynthetically active radiation and heat which are incident upon the leaf surfaces. It is frequently assumed that the preferred orientation is perpendicular to the strongest illumination.

Most reports of solar tracking have emphasized the ability of leaves to orient with their surfaces directly facing the sun so that the amount of solar radiation absorbed is maximized (Shell & Lang, 1975; Wainwright, 1977; Schwartz & Koller, 1978;

Forseth & Ehleringer, 1980).

For plants in which there is little or no daily movement of leaf surfaces, the fixed orientation of leaves results from cumulative effect of incident solar radiation which is changed each time at the solar elevation and azimuth. Most reports on the solar radiation incident on a leaf surface have treated the angle of incidence, θ, of direct solar radiation upon a photosynthetic surface (Shell *et al.*, 19 74; Kirkham, 1982; Herbert, 1983; Travis & Reed, 1983; Kirkham, 1984). The angle is one between a normal vector to that surface and a vector pointing in the direction of the incident radiation, so that the cosine of the angle of incidence represents the fraction of the maximum direct solar radiation which the photosynthetic surface can intercept. This angle is changed on a leaf surface with the fixed angle with respect to the solar elevation and azimuth, which are varied each time. In order to determine the leaf orientation which receives the maximum radiation during a day, it is needed to integrate the instantaneous radiation from the hour of sunrise to that of sunset.

This paper presents the theoretical model for monthly average daily solar radiation intercepted upon a leaf with a slope and an azimuth angle. Our purposes are to determine the leaf orientation in which sum of daily radiation is maximized during the growing season and to compare the observed distribution of leaf angles in various plant species.

MATERIALS AND METHODS

Theoretical: In order to describe and qualify the leaflet movement responses, a geometrical model of the leaflet was used.

Insolation on clined leaf was computed using equations (8) and (9), within the limits of direct component without regard to transmittance through the atmosphere.

Experimental: Studies were conducted in field condition at Mt. Jiri, Korea from 24 to 26, August, 1981~1984. Leaves of ginkgo(*Ginkgo biloba* Linné) and maple tree (*Acer palmatum* Thunberg) were selected to receive full sunlight, i.e., they were not shadowed by other leaves orplant organs.

Inclinations above or below the horizontal were measured with a hanging pointer device calibrated to read 0° at the horizontal and ±90° at the vertical. Azimuths were measured with a compass.

THEORETICAL MODELS

Radiation components on the leaf surface

The flux of PAR upon a tilted leaf surface consist of three contributions. (1) The flux of direct solar PAR, (2) The flux of diffuse sky PAR and (3) The part of reflected PAR by the ground underlying the atmosphere which is incident on the tilted leaf surface. Each one of these contributions depends on the geographical coordinates, cloud coverage, the solar altitude and the optical properties of the atmosphere and underlying surface. These fluxes shall be considered by the analogous methods of Jimenez and Castro (1982) separately.

(1) Direct solar PAR: For purposes of calculating the photosynthetically active radiation(PAR) on a leaf, it is often necessary to convert data for PAR on a horizontal surface to radiation on a tilted surface.

Fig. 1. PAR on horizontal(A) and tilted leaf surfaces(B)

The PAR on a horizontal leaf surface, I, is $I_n \cos\theta_z$, and that on a tilted leaf surface, I_t, is $I_n \cos\theta_T$. The ratio of PAR of a tilted leaf surface to that on the horizontal one, Rb, is given in terms of the angles θ_z and θ_T, and PAR normal to the beam, I_n, by

$$Rb=\frac{I_t}{I}=\frac{I_n \cos\theta_T}{I_n \cos\theta_z}=\frac{\cos\theta_T}{\cos\theta_z} \qquad (1)$$

(2) Diffuse sky PAR: The correction factor for

the diffuse radiation component depends on the distribution assumed of them over the sky. In this work the Liu and Jordan's hypothesis was assumed, taking into account that this component is uniformly distributed over the sky dome(Liu and Jordan, 1963; Duffie and Beckman, 1974). Thus, a leaf surface tilted a slope angle S from the horizontal "sees" a portion of the sky dome given by

$$I_{ds}=\frac{1+\cos S}{2}I_d \quad \cdots\cdots(2)$$

being I_{ds} the flux of diffuse PAR incident on a leaf plane tilted a slope angle S in any orientation and I_d the one on a horizontal plane.

(3) Ground reflection of PAR: Also with the assumed hypothesis, the sloped surface "sees" a portion of the ground and the surface receives the PAR reflected from it. Assuming a diffuse reflectance for the surroundings, the value of reflected PAR, I_{rs}, incident on a tilted leaf plane, is

$$I_{rs}=\frac{1-\cos S}{2}(I+I_d)\rho \quad \cdots\cdots(3)$$

where I is the direct solar PAR on horizontal plane. Combining the three terms, the total solar PAR on the tilted leaf surface at any time is

$$I_{ts}=IR_b+I_{ds}+I_{rs}$$
$$=IR_b+\frac{1+\cos S}{2}I_d+\frac{1-\cos S}{2}(I+I_d)\rho \quad \cdots\cdots(4)$$

Geometric relation between the direct radiation and the leaf orientation: When the leaf orientation is determined by a vector relationship between the external stimulus such as light and the response organ, the direct solar radiation

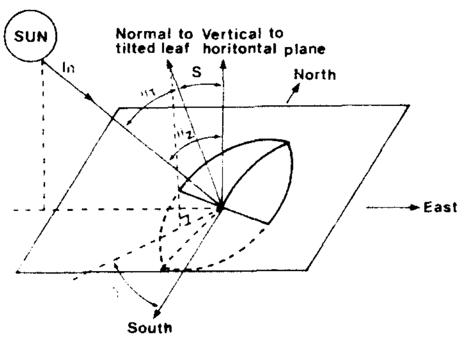

Fig. 2. Definition of solar and surface angles for a non-south-facing tilted leaf.

plays a major role in orienting the leaves. The angle of incidence, θ_T, of direct solar radiation upon a photosynthetic surface is the angle between a normal vector to that surface and a vector pointing in the direction of the incident radiation.

The geometric relationships between a leaf of any particular orientation relative to the earth at any time and the incoming beam solar radiation can be described in terms of several angles.

$$\cos\theta_T=\sin\delta\sin\phi\cos S-\sin\delta\cos\phi\sin S\cos\gamma$$
$$+\cos\delta\cos\phi\cos S\cos\omega$$
$$+\cos\delta\sin\phi\sin S\cos\gamma\cos\omega$$
$$+\cos\delta\sin S\sin\gamma\sin\omega \quad \cdots\cdots(5)$$

$$\cos\theta_z=\sin\delta\sin\phi+\cos\delta\cos\phi\cos\omega \quad \cdots\cdots(6)$$

where

ϕ : latitude (north positive)

δ : declination (north positive)

S : the angle between the horizontal and the plane (i.e. the slope)

γ : the surface azimuth angle, that is, the deviation of the normal to the surface from the local meridian, the zero point being due south, east positive, and west negative.

ω : hour angle, solar noon being zero, and each hour equaling 15° of longitude with morning negative and afternoon positive.

θ : the angle of incidence of beam radiation, the angle being measured between the beam and the normal to the plane.

The declination, δ can be found from the approximate equation of Cooper (1969) :

$$\delta=23.45\sin\left(360\frac{284+n}{365}\right)$$

where n is the day of the year.

Estimation of daily radiation as a monthly mean value: The monthly average daily radiation on a tilted leaf surface, $\bar{I}_{ts}$, is given from eqn(5) (Lin & Jordan, 1963)

$$\bar{I}_{ts}=(\bar{I}-\bar{I}_d)R_b+\bar{I}_d\frac{(1+\cos S)}{2}+\bar{I}\rho\frac{(1-\cos S)}{2} \quad (7)$$

where $\bar{I}$ is the monthly average daily radiation on a horizontal surface, $\bar{I}_d$ is the monthly average daily diffuse radiation, and $\bar{R}_b$ was estimated by integrating the rate of extraterrestrial radiation on the leaf surface for the period during which the sun is above the horizon and in front of the leaf surface and then diving this result by $\bar{I}_0$, the mean daily extraterrestrial radiation on a horizontal surface (Klein, 1977)

$$\bar{R}_b=\frac{\int_{w_{sr}}^{w_{ss}} I_t d\omega}{\int_{w_{sr}}^{w_{ss}} I_0 d\omega}=\frac{\int_{w_{sr}}^{w_{ss}} \cos\theta_T d\omega}{\int_{w_{sr}}^{w_{ss}} \cos\theta_z d\omega}$$

$$=((\cos S\sin\delta\sin\phi(w_{ss}-w_{sr})\pi/180$$
$$-(\sin\delta\cos\phi\sin S\cos\gamma)(w_{ss}-w_{sr})\pi/180$$
$$+(\cos\phi\cos\delta\cos S)(\sin w_{ss}-\sin w_{sr})$$
$$+(\cos\delta\cos\gamma\sin\phi\sin S)(\sin w_{ss}-\sin w_{sr})$$
$$-(\cos\delta\sin S\sin\gamma)(\cos w_{ss}-\cos w_{sr}))$$
$$/(2(\cos\phi\cos\delta\sin W_s+\pi/180\,W_s\sin\phi\sin\delta))\cdots(8)$$

where w_{sr} and w_{ss} are the sunrise and sunset hour angles on the tilted surface and W_s is the sunset hour angle on the horizontal surface, given by:

if $\gamma<0$

$$w_{sr}=-\min(W_s,\ \arccos((AB+\sqrt{A^2-B^2+1})/(A^2+1)))$$

$$w_{ss}=\min(W_s,\ \arccos((AB-\sqrt{A^2-B^2+1})/(A^2+1))) \cdots\cdots(9)$$

if $\gamma\geq0$

$$w_{sr}=-\min(W_s,\ \arccos((AB-\sqrt{A^2-B^2+1})/(A^2+1)))$$

$$w_{ss}=\min(W_s,\ \arccos((AB+\sqrt{A^2-B^2+1})/(A^2+1))) \cdots\cdots(10)$$

$$A=\cos\phi/(\sin\gamma\tan S)+\sin\phi/\tan\gamma \cdots\cdots(11)$$

$$B=\tan\delta(\cos\phi/\tan\gamma-\sin\phi/(\sin\gamma\tan S)) \cdots\cdots(12)$$

$$W_s=\arccos(-\tan\phi\tan\delta) \cdots\cdots(13)$$

In this study the mathematical model of monthly average daily radiation was established, and the direct light incident on a tilted leaf surface with any azimuth angle was calculated by FORTRAN LANGUAGE in order to determine the leaf orientation receiving the maximum irradiance each month, during the growing season and for an year. Leaf angles were practically measured and their distribution was compared with the theoretical one.

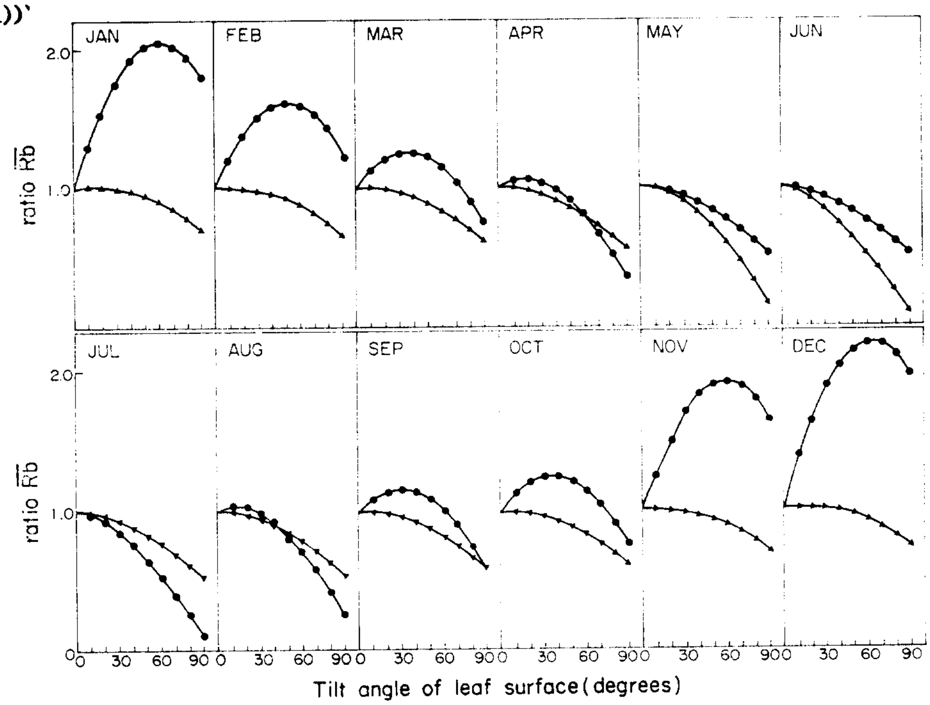

Fig. 3. Effect of leaf tilt on the intercepted direct solar radiation. The ratio, $\bar{R}_b$, of monthly mean direct radiation on the tilted leaf surface to that on the horizontal was calculated each month according to the surface azimuth angle; south facing leaf (●—●) and due east or due west facing one (▲—▲).

RESULTS AND DISCUSSIONS

The solar orientation changes momently during a day as well as for an year, and then the geometric relationship between the sun and the tilted leaf surface with a certain azimuth is consequently altered. To quantify the direct solar radiation the angle of incidence is used effectively. The ratio of the cosine of the angle of the incidence on a tilted surface to that on the horizontal, R_b, represents the relative intensity of direct solar radiation according to the surface orientation. To determine the leaf orientation received maximum radiation during a day, monthly mean daily ratio $\overline{R}_b$ was calculated from equation (9) as a function of the leaf elevation on the leaf surface facing south and facing due east or due west respectively (Fig. 3). The

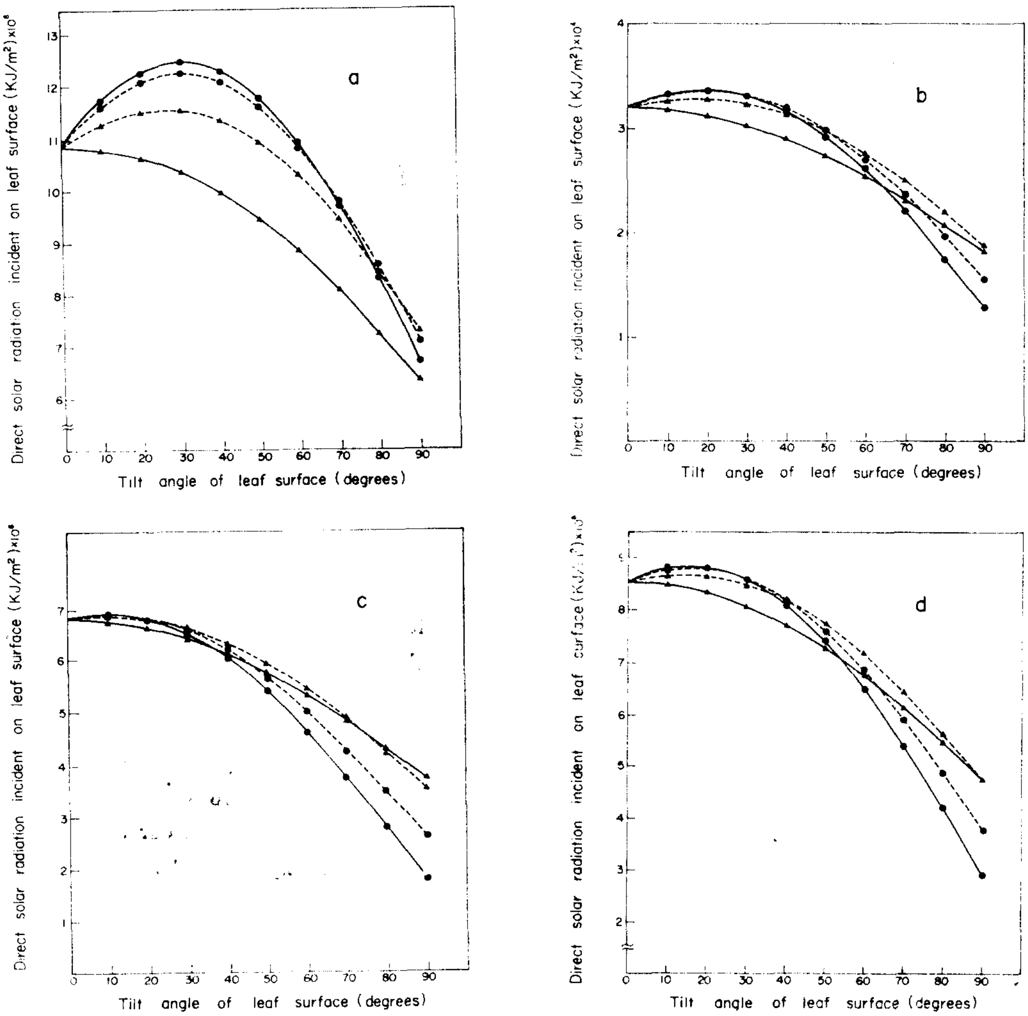

Fig. 4. Effect of leaf tilt on the intercepted direct solar radiation which was calculated for an year (a), from March to May (b), from March to August (c), and from March to October (d) according to the surface azimuth angles; south facing leaf (●—●), due east or due west facing one (▲—▲), the leaf of surface normal azimuth angle being ±30° from the south (●···●), and that being ±60° (▲···▲).

direct solar radiation incident on a leaf surface facing south was maximized at the leaf elevation of 50°~60° in the winter, at that of 20°~40° in the spring and autumn, and at the horizontal leaves in the summer. While due east or west facing leaf showed the maximum value at the horizontal orientation through an year.

Most leaves of various plants exist through the growing season. It has not been explained whether their orientations were affected continuously by the direct radiation or they were determined at the beginning of growth. The direct solar radiation incident on a leaf surface was calculated for an year, from March to May, from March to August, and from March to October(Fig. 4). Because our purpose is to compare the relative intensity of direct solar radiation according to the changes of leaf angles, the transmittance through the atmosphere was neglected. The intensity of direct solar radiation for an year was maximized at the leaf elevation of 20°~40° except the leaf surface facing due east or due west. But the direct radiation incident leaf surfaces from March to May, from March to August, and from March to October showed less remarkable changes than the yearly total according to the surface azimuth. The maximum value was gained at the elevation of 0°~20° at these periods, and on the whole leaves with the tilt angle of 0° ~40° received much radiation comparing with those of other tilt angles.

The theoretical tendency of direct solar radiation was compared with the practical distribution of leaf orientations. We have attempted to collect and bring into a pattern on leaf orientation both from the literature and our own (Table 1 and Fig. 5). We exercised the quantitative measurement of the angular distribution in the 2 species ginkgo and maple tree. Most leaves taken for our purpose were flattened in their shape and receiving in full sunlight. The average leaf elevation of maple tree was 17.0°±12.0°, and that of ginkgo tree was 29.8°±16.0°. Our results showed that leaf arrangement was largely horizontal and most leaves were in the range of elevation of 0°~50° in both trees. It is supported well by our theoretical tendency of radiation incident on a tilted leaf surface. In Korea most leaves come out in April and they grow up through the spring, summer, and autumn. The incident direct solar radiation showed the maximum on the surface with tilt angle of 0°~40° all the periods from March to June, from March to August, and from March to October (Fig. 4-b, c, d).

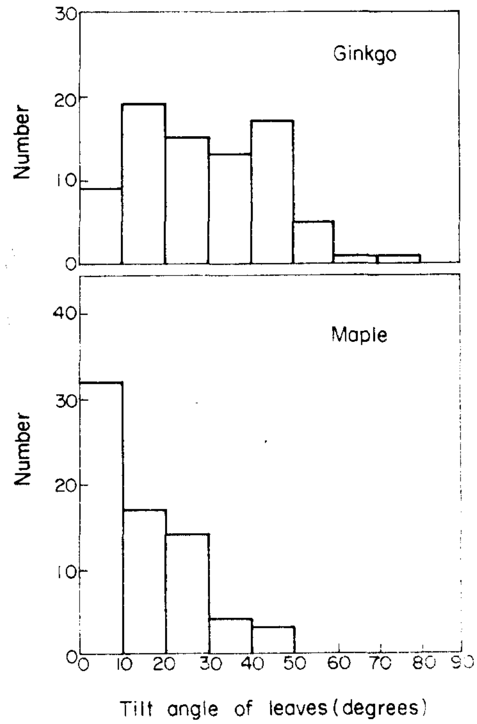

Fig. 5. The distribution of leaf tilt angles in Ginkgo and Maple treess.

Many other resuts support our theoretical tendency (Table 1). Experimental regions were in different latitude but theoretical teudencies were different little(The data were not presented here). Many authors insisted on the non-random orientation of leaves (Nichiporovichi, 1961; de Wit, 1965; Ross & Ross, 1969; Shell et al, 1974; Shell & Lang, 1975; Mc Millen & Mc Clendon, 1979). More than 80 % of leaves were tilted within 60° from the horizontal (Table 1). The heliotropic plants, sunflower,

Table 1. Leaf inclination in stands of different species

Plants	Region	Date & Time	Layer(m)[a]	Inclination deg.[b] 0~30	30~60	60~90	Original Paper
Straw berry	Moscow			0.66	0.19	0.15	Nichiporovichi(1961)
White clover	Moscow			0.70	0.20	0.10	Nichiporovichi(1961)
White clover	Holland	Aug. 21		0.54	0.41	0.05	de Wit(1965)
Sun flower	Japan	July 17		0.55	0.37	0.08	Ross & Ross(1969)
Horse beans	Estonia	Aug. 1		0.30	0.50	0.20	Ross & Ross(1969)
Potato	Moscow			0.40	0.37	0.23	Nichiporovichi(1961)
Potato	Holland	May 28		0.57	0.38	0.05	de Wit(1965)
Cucumber	Moscow			0.52	0.37	0.11	Nichiporovichi(1961)
Sweet chestnut	U.K.	May 17	6.5~7.0	—	—	—	Ford & Newbould(1971)
		July 27	6.0~6.5	3	—	—	
		Aug. 25	5.5~6.0	10	4	4	
			5.0~5.5	20	29	31	
			4.5~5.0	8	35	35	
			4.0~4.5	2	14	12	
			3.5~4.0	—	1	1	
			3.0~3.5	—	—	—	
				Mean value			
Sun flower	Australia	a.m.		34			Shell *et al.*(1974)
		mid		30			
		p.m.		30			
Sun flower	Australia			29~42			Shell & Lang(1975)
Bean	Australia	a.m.		38			Shell *et al.*(1974)
		mid		42			
		p.m.		39			
Pepper	Australia			47			Shell *et al.* (1974)
Cucumber	Australia			32			Shell *et al.* (1974)
Cotton	California			0~30			Fukai & Loomis(1976)
				Sun	Shade		
Cotton wood	Nebraska			75.7± 7.8	32.3±19.8		McMillen & Mc Clendon (1979)
Plum				33.4±15.5	16.4±12.4		
Kentucky coffee tree				64.5±19.2	10.2± 7.0		
Catalpa				24.2±15.0	8.2± 6.4		
Red bud				35.9±18.8	13.8±14.2		
Green ash				36.8±18.9	14.4±13.8		
Red oak				10.1±10.9	11.5± 8.2		
Mulberry				34.0±15.4	10.6± 8.4		
Silver maple				16.9±15.5	12.7± 9.8		
Sugar maple				14.6±10.2	7.8± 5.5		

a. Layer represents the height above ground level. The inclination degree of leaves was examined at each 0.5m height interval through the canopy.

b. The relative frequencies of leaves inclined at each range of 0°~30°, 30°~60°, and 60°~90° from the horizontal were represented.

bean, pepper and cucumber, showed the preferred mean elevation and their azimuth angles represented the tendency for leaves to face east during the morning and to turn with the sun and disperse somewhat as the day proceeds (Lang, 1973; Shell & Lang, 1975).

Mc Miller & Mc Clendon(1979) have not seen any systematic characterization of species which indicates that light might be a more common factor in individual adaptation. But all plants selected by them showed the horizental tendency of their leaf orientation under the shade screen. Under the full sunlight leaves showed horizontal tendency in several species and other species did not. But the leaves under the full sunlight were V-shaped or twisting of the petioles, and therefore it is thought that there might be the problems in measuring the leaf angles or other factors affecting the leaf growth.

A research of woodland structure showed that foliage was horizontal at the top and bottom of the canopy but angled in the middie(Ford & Newbould, 1971). The penetration of light into the leaf canopy is influenced by leaf amount, leaf angle, leaf dispersion and the light transmission characteristics of leaves. Estimation of the orientation of a single leaf is different from that of whole canopy, but most leaves selected in this research had the elevation angle within 30° from the horizontal. The increase in photosynthetic efficiency has an effect on the total photosynthesis of the plant and this is not easy to quantify as an unique orientation.

The analysis presented here does not consider concretely many important factors which will affect the interception and absorption of light by photosynthetic surface. Radiation absorbed from diffuse skylight or reflected from the ground was included in eqation (2) and (3) of our mathematical model but it was not calculated by computer simulation.

The direct component of solar radiation was surveyed using the model, and then the leaf orientation of maximum irradiance could be determined. Practical orientation of leaves in various plants corresponded with the orientation expected theoretically in which leaf surfaces receive the maximum direct solar radiation during the growing season. It is suggested that cumulative effect of relation between surface normal vector and a vector pointing in the direction of the radiation determine the leaf orientation. Of course all cases are not explained by this suggestion.

摘 要

光合成有効放射(PAR)는 植物의 光合成과 生長速度에 큰 영향을 미치게 되므로 太陽光線을 받는데 있어서 葉表面의 方位別 傾斜度는 대단히 중요하다. 本 研究에서는 이에 대한 數理 model을 定立하고, 이에 따라 最大로 受光되는 葉位를 구하였다. 이를 月別로 計算한 結果, 겨울에는 50~60°로 傾斜진 잎에서, 봄·가을에는 20~40°의 잎에서 그리고 여름에는 水平인 잎에서 最大의 受光量을 나타내었다. 生長期와 一年을 通算하여 算出된 결과로는 각각 0~20°와 20~40°로 傾斜진 잎에서 각기 最大 受光量을 나타내었다. 全般的으로 볼 때, 0~40°범위의 傾斜角을 가진 잎의 경우에 이 以上의 傾斜角을 가진 잎에 比하여, 그 受光量이 현저히 높았다.

이와 아울러 實測된 葉位의 分布를 比較해 보면, 단풍나무에서는 잎의 平均傾斜角이 17.0±12.0°이었으며, 은행나무의 경우는 平均 29.0±16.0°이었다. 다른 參考文獻에서 調査된 結果도 이와 類似한 分布를 나타내었으므로, 葉表面의 垂直vector와 放射方向의 vector 사이의 關係가 一定期間 累積되어 最大의 受光條件을 갖추도록 葉位가 決定된다고 推定된다.

REFERENCES

Cooper, P.I., 1969. The Absorption of Solar Radiation in Solar Stills. Solar Energy, **12** : 333~346.

Duffie, J.A. and W.A. Beckman, 1974. Solar Energy Thermal Processes. Wiley, New York.

Ford, E.D. and P.J. Newbould, 1971. The Leaf Canopy of a Coppiced Deciduous Woodland. Jour. Ecol., **59** : 843~862.

Forseth, I. and J.R. Ehleringer, 1980. Solar Tracking Response to Drought in a Desert Annual. Oecologia (Berl.), **44** : 159~163.

Fukai, S. and R.S. Loomis, 1976. Leaf Display and Light Environments in Row Planted Cotton Communities. Agric. Meteorol., **17** : 353~379.

Herbert, T.J., 1983. The Influence of Axial Rotation upon Interception of Solar Radiation by Plant Leaves. J. Theor. Biol., **105** : 603~618.

Jimenez, J.I. and Y. Castro, 1982. Solar Radiation on Sloping Surfaces with Different Orientations in Granada, Spain. Solar Energy, **28** : 257~262.

Kirkham, M.B., 1982. Orientation of Leaves of Winter Wheat Planted in North-South or East-West Rows. Agron. J., **74** : 893~898.

Kirkham, M.B., 1984. Leaf Orientation, Light Reception, and Growth of Winter Wheat. Crop Sci., **24 : 925~928.**

Klein, S.A., 1977. Calculation of Monthly Average Insolation on Tilted Surfaces. Solar Energy, **19** : 325~329.

Lang, A.R.G., 1973. Leaf Orientation of a Cotton Plant. Agric. Meteorol., **11** : 37~51.

Liu, B.Y.H. and R.C. Jordan, 1963. The Long Term Average Performance of Flat-Plate Solar Energy Collectors. Solar Energy, **7** : 53~74.

Mc Millen, G.G. and J.H. Mc Clendon, 1979. Leaf Angle: an Adaptive Feature of Sun and Shade Leaves. Bot. Gaz., **140** : 437~442.

Nichiporovich, A.A. 1961. On Properties of Plants as an Optical System. Sov. Plant Physiol., **8** : 536~546.

Ross, J. and V. Ross, 1969. Spacial Orientation of Leaves in Crop Stands. In: Photosynthetic Productivity of Plant Stand; 69~82. Acad. Sci. ESSR, Inst. Phys. Astron., Tartu.

Schwartz, A. and D. Koller, 1978. Phototropic Response to Vectorial Light in Leaves of *Lavatera cretica* L. Plant Physiol., **61** : 924~928.

Shell, G.S.G. and A·R.G. Lang, 1975. Description of Leaf Orientation and Heliotropic Response of Sunflower using Directional Statistics. Agric. Meteorol., **15** : 33~48.

Shell, G.S.R., A.R.G. Lang and P.J.M. Sale, 1974. Quantitative Measures of Leaf Orientation and Heliotropic Response in Sunflower, Bean, Pepper, and Cucumber. Agric. Meteorol., **13** : 25~37.

Travis, R.L. and R. Reed, 1983. The Solar Tracking Pattern in a Closed Aifalfa canopy. Crop Sci., **23** : 664~668.

Wainwright, C.M., 1977. Sun-Tracking and Related Leaf Movements in a Desert Lupine (*Lupinus arizonicus*). Amer. J. Bot., **64** : 1032~1041.

Wit, C.T., de, 1965. Photosynthesis of Leaf Canopies. Agric. Res. Report No. 663, Wageningen; 1~57.

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