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Adaptive Responses of Soybean and Cotton to Diurnal Changes in Solar Radiation and Leaf Movement

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Abstract: Adaptive responses to diurnal changes in solar radiation and leaf movement restraint in soybean in comparison with cotton, which observes different heliotropism from that of soybean, were investigated in terms of leaf temperature (T_L), Flow Rate of Stem Sap (FRSS), transpiration rate (E), stomatal conductance (g_s) and stomatal aperture. Cotton showed higher FRSS and E while smaller T_L than that of restrained (RLM) and Not-restrained Leaf Movement (NRLM) soybean. The RLM soybean showed higher FRSS, E at noon and T_L than that of NRLM soybean. Larger FRSS and E of cotton could be attributed to its higher stomatal density, stomatal aperture, g_s and the diaheliotropic leaf movement. In NRLM soybean, smaller FRSS and smaller E at noon as compared with RLM soybean might be due to the smaller abaxial stomatal aperture, g_s and the paraheliotropic leaf movement. It was concluded that cotton responded to increase in diurnal solar radiation by increasing its transpiration to reduce T_L . Increase in transpiration of cotton was due to increase in the size of stomatal aperture, g_s and the diaheliotropic leaf movement. NRLM soybean responded to increase in solar radiation by observing paraheliotropism in order to reduce its T_L while RLM soybean increased its transpiration in order to reduce T_L . Increase in transpiration of RLM soybean was due to increase in abaxial stomatal aperture.

Key words: Adaptive responses, *Glycine max* (L.) Merr., *Gossypium hirsutum* L., leaf movement, leaf temperature, solar radiation, stomatal conductance, transpiration

INTRODUCTION

Previous studies have reported that paraheliotropic leaf movement minimizes the interception of solar radiation incident on a leaf (Isoda and Wang, 2002) with consequent reductions in leaf temperature (Isoda *et al.*, 1994) and the rate of water loss (Isoda and Wang, 2002). Thus paraheliotropism contributes substantially to both heat and drought avoidance.

Paraheliotropic leaf movement and high transpiration both have been reported as plants' strategies to avoid drought and heat stress (Bressan, 2002) probably because both of these two strategies lead to a decrease in leaf temperature (Isoda *et al.*, 1994; Pettigrew, 2004). Larger increase in leaf temperature of soybean was observed when its leaf movement was restrained in the upper crop canopy (Isoda and Wang, 2001).

Heliotropic leaf movements regulate the amount of water loss (transpiration), leaf temperature and photosynthesis in soybean and cotton (Isoda *et al.*, 1994; Isoda and Wang, 2001; 2002; Wang *et al.*, 2004b; Inamullah and Isoda, 2005). However, there are very few reports regarding adaptive changes in transpiration, stomatal aperture, stomatal conductance and leaf temperature of soybean if its leaves were prevented from

heliotropic leaf movement. Furthermore, there is almost no report showing diurnal adaptive changes in field-grown soybean and cotton in response to diurnal changes solar radiation. The underlying hypothesis is that the two crops may exhibit different responses because they perform different heliotropic leaf movements at midday (Wofford and Allan, 1982; Ehleringer and Forseth, 1989). The objective of this experiment was to study various adaptive changes in soybean at various times of the day when its leaf movement was restrained in comparison with cotton and soybean that could move their leaves freely.

MATERIALS AND METHODS

The experiment was conducted in field at the Faculty of Horticulture, Chiba University, Matsudo (35°47' North Latitude, 139°54' East Longitude and Altitude 23.2 meters), Chiba, Japan, in summer 2003. Soybean cultivar Tachinagaha and cotton cultivar Xinluzao-8 were sown on June 9 in rows 30 cm apart having plant-to-plant distance of 30 cm. The experiment was sown in an RCB design having three replications. Each replication had three subplots, in which cotton, soybean with leaf movement not-restrained, hereafter called NRLM and soybean with leaf movement restrained, hereafter called RLM, were

sown. Each subplot had an area of 49 m². Leaf movement in the upper canopy of RLM soybean was restrained with a 0.55 mesh nylon net in a 9 m² area at the pod setting stage, R3 (Fehr and Caviness, 1977) on Aug 10. Diurnal changes in leaf temperature (T_L) and flow rate of stem sap (FRSS) were examined for several days. The data of the day with the most suitable weather conditions (Aug 30) are shown. During data collection, soybean was at the beginning of seed development stage, R5 (Fehr and Caviness, 1977) and cotton at the boll formation stage.

T_L, transpiration rate (E), stomatal conductance (g_s), stomatal density and aperture and CO₂ assimilation rate (A_N) were measured on terminal leaflet of the mainstem in soybean and on first fully expanded leaf at the top of the plant in cotton. Diurnal changes in T_L were measured using thermocouples. Thermocouples were attached to abaxial sides of the selected leaves. Data were collected at one-minute intervals from 600 to 1800 h with a datalogger (Eto Denki Inc., Japan) connected to a personal computer. T_L was also measured along with E and A_N using LI-6400 Photosynthetic Measurement Systems (LI-COR, Lincoln, USA). FRSS was measured with stem sap flow gauge (Dynamax Inc., USA) using stem heat balance method (Sakuratani, 1981). Sap flow gauges were attached tightly around the stems of the plants at the base above the soil surface. Each gauge was covered with an aluminum foil to reduce the effects of external radiation on the heat balance of the stem. Each gauge was connected with dataloggers, which collected FRSS data simultaneously with T_L. The same dataloggers were used for collecting the air temperature, Photosynthetically Active Radiation (PAR) and relative humidity data also.

Stomatal data were collected according to Hirose *et al.* (1992). Data were collected in the morning (0900 h), noon (1200 h) and afternoon (1500 h) on three cover glasses in three plants per treatment. The stomata were counted in three randomly chosen microscope fields from each impression on the cover glass and thus 27 microscope fields were examined for determining stomatal density in each treatment. Each microscope field had an area of 0.6003 mm² at 100 X magnifications. The stomatal aperture was measured on photoprints taken at 400 X magnifications according to Wise *et al.* (2000). Five stomata were randomly selected from each of the 27 prints for studying stomatal aperture and thus 135 stomata were studied for calculating stomatal aperture in each treatment.

Stomatal conductance (g_s), E, T_L and A_N were measured in the morning (900 h), noon (1200 h) and afternoon (1500 h) using LI-6400 Photosynthetic Measurement Systems (LI-COR, Lincoln, USA). All data were analyzed using Genstat 5 (Lawes Agric. Trust,

Rothamsted, 1998). The significant differences between treatments were determined using Duncan's Multiple Range test.

RESULTS

Climatic conditions: Maximum PAR of 1484 μmol sec⁻¹ m⁻² was recorded around 1300 h along with maximum air temperature of 28.4°C. Minimum relative humidity of 66.3% was recorded at the same time (Fig. 1). Relative humidity changed negatively with changes in PAR during the whole day.

Diurnal changes in flow rate of stem sap per unit leaf area (FRSS): FRSS of cotton was higher than that of soybean during the whole day (Fig. 2A). FRSS of RLM soybean was a little higher than that of NRLM soybean; however, around 900 h and at midday when light intensity was higher, larger increase was observed in FRSS of RLM soybean as compared with NRLM soybean. Cotton recorded maximum FRSS value of 2.2 g dm⁻² h⁻¹ at 1335 h, while RLM and NRLM soybean recorded maximum FRSS values of 2.0 and 1.7 g dm⁻² h⁻¹ at the same time, respectively.

Diurnal changes in leaf temperature (T_L): Diurnal changes in T_L measured with thermocouples showed that cotton's T_L was lower than that of soybean, however, it was higher than the air temperature during most part of the day especially at midday (Fig. 2B). Soybean's T_L under RLM was larger than that under NRLM. Soybean

Table 1: Stomatal density of cotton and soybean in restrained (RLM) and not-restrained leaf movement (NRLM)

Crop	Stomatal density (mm ⁻²)	
	Abaxial	Adaxial
Soybean (NRLM)	191b	125b
Soybean (RLM)	199b	119b
Cotton	339a	171a

Means in the same category followed by different letters are significantly different at 5%

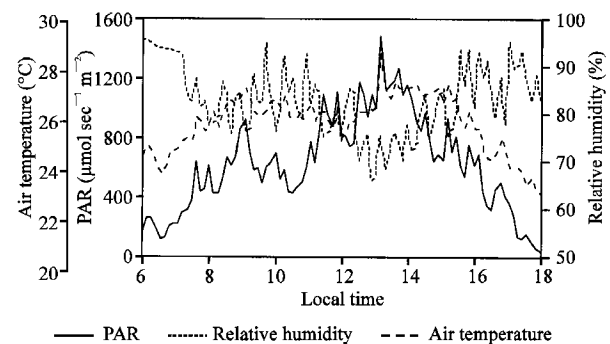


Fig. 1: Climatic conditions in Matsudo on Aug. 30, 2003

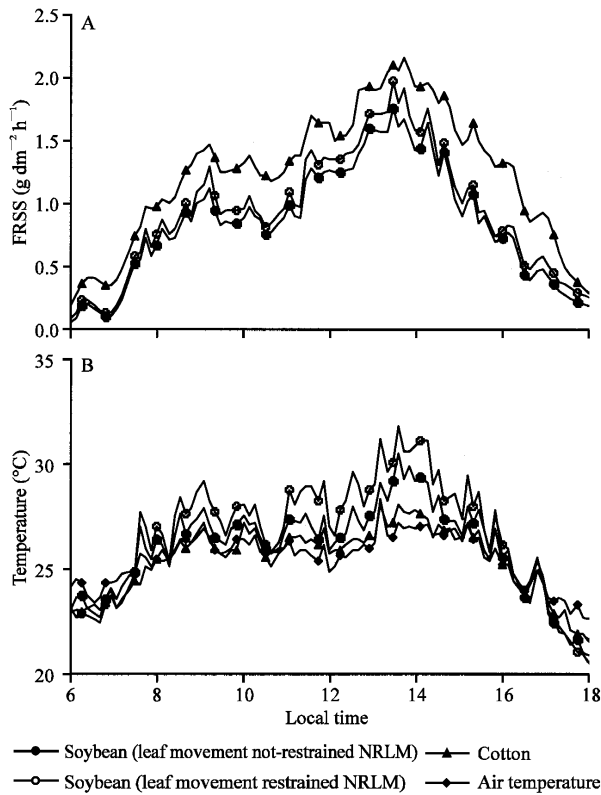


Fig. 2: Diurnal changes in flow rate of stem sap per unit leaf area (FRSS) (A) and leaf temperature (B) of cotton and soybean (NRLM and RLM) grown under field conditions. This figure shows average of every 5 min data collected from 0600 to 1800 h on Aug. 30, 2003

Table 2: Leaf temperature (TL) and stomatal aperture of cotton and soybean in restrained (RLM) and not-restrained leaf movement (NRLM) in the morning (0900 h), noon (1200 h) and afternoon (1500 h)

Time (h)	Crop	Leaf Temp. (°C)	St. Aperture (µm)	
			Abaxial	Adaxial
0900	Soybean (NRLM)	34.3d	3.5def	3.31d
	Soybean (RLM)	34.3d	3.4ef	3.24d
	Cotton	33.2e	4.6c	7.5a
1200	Soybean (NRLM)	37.4b	4.1cd	4.1c
	Soybean (RLM)	40.3a	5.2b	4.5c
	Cotton	35.2c	6.0a	8.0a
1500	Soybean (NRLM)	35.3c	3.18f	3.04d
	Soybean (RLM)	36.8b	3.13f	2.77d
	Cotton	34.0de	3.9de	4.5c

Means in the same category followed by different letters are significantly different at 5%

recorded maximum T_L of 31.9°C under RLM and 30.6°C under NRLM around 1335 h. Cotton's T_L and air temperatures were same at this time i.e., 28.2°C.

T_L measured with LI-6400 (LI-COR, USA) in the morning (900 h), noon (1200 h) and afternoon (1500 h) showed significantly larger increase in RLM soybean

as compared with NRLM soybean and cotton at noon (Table 2). Cotton's T_L was 33.2°C in the morning, significantly lower than those of RLM and NRLM soybean (34.3°C in both cases). At noon, RLM soybean's T_L increased to 40.3°C while T_L of cotton and NRLM soybean increased to 35.2 and 37.4°C, respectively. In the afternoon, T_L of cotton and soybean in RLM and NRLM decreased to 34, 36.8 and 35.3°C, respectively. Cotton's T_L was significantly lower than those of soybean at all times of the day. T_L of RLM soybean was not significantly different from that of NRLM in the morning. At noon and in the afternoon, however, T_L of RLM soybean was significantly higher than that of NRLM soybean. Furthermore, in the morning T_L in both crops was significantly lower than that in the afternoon.

Stomatal density: Stomatal density on both abaxial and adaxial leaf surfaces in cotton leaves was higher than that of soybean (Table 1). On abaxial leaf surface the stomatal density of cotton was 339 mm⁻² while that of soybean was 199 and 191 mm⁻² under RLM and NRLM, respectively. On adaxial surface cotton showed 171 stomata per mm² while soybean showed 119 and 125 stomata under RLM and NRLM, respectively. Stomatal density in soybean did not differ significantly under RLM and NRLM on adaxial as well as abaxial leaf surfaces. Stomatal density on abaxial leaf surfaces was greater as compared with the adaxial leaf surfaces in both crops. However, in cotton the difference was larger.

Stomatal aperture: Stomatal aperture at abaxial leaf surface (Table 2) in cotton was significantly larger than that of RLM and NRLM soybean at various times of the day. Significantly larger increase was observed in abaxial stomatal aperture in cotton at noon (6 µm) as compared with morning (4.6 µm) and afternoon (3.9 µm). The afternoon, abaxial stomatal aperture of cotton was significantly smaller than that in the morning. In the morning, the size of abaxial stomatal aperture in soybean was not significantly different under RLM and NRLM (3.4 and 3.5 µm), respectively and same was the case in the afternoon also (3.13 and 3.18 µm), respectively. However at noon, abaxial stomatal aperture increased significantly under RLM (5.2 µm) and this increase was significantly larger than that in the NRLM soybean (4.1 µm). The increase in abaxial stomatal aperture of NRLM soybean at noon was not significantly different from that in the morning; however, it was significantly larger than that in the afternoon. The morning abaxial stomatal aperture size in soybean was not significantly different from that in the afternoon both under RLM and NRLM.

Adaxial leaf stomatal aperture (Table 2) in cotton was also significantly larger than that in soybean (RLM and NRLM) at various times of the day. The size of adaxial stomatal apertures was significantly larger in cotton in the morning (7.5 μm) and at noon (8 μm). In the afternoon, adaxial stomatal aperture in cotton decreased significantly to 4.5 μm . In soybean (RLM and NRLM), adaxial stomatal apertures did not differ significantly from each other at all times of the day. In the morning, the size of adaxial stomatal aperture was 3.24 and 3.31 μm under RLM and NRLM, respectively, which increased significantly to 4.5 and 4.1 μm , respectively, at noon. In the afternoon, it decreased again significantly to 2.77 and 3.04 μm , respectively. The size of adaxial stomatal aperture in the morning was not significantly different from that in the afternoon in RLM and NRLM soybean.

Stomatal conductance (g_s) and transpiration rate (E):

Stomatal conductance (g_s) (Table 3) and transpiration rate (E) (Table 3) of cotton were significantly higher than that of soybean (RLM and NRLM) at various times of the day. g_s and E increased significantly in both crops at noon and the increase was significantly larger in cotton, followed by the RLM and NRLM soybeans, respectively. In the afternoon, g_s and E decreased significantly in both crops. The afternoon g_s and E in cotton were significantly lower than the g_s and E in the morning. In soybean, g_s and E of the RLM and NRLM treatments did not differ in morning and afternoon.

Correlation of T_L with stomatal aperture, g_s and E:

T_L showed positive correlation with stomatal aperture in both crops at various times of the day. However, the correlation between T_L and abaxial stomatal aperture was significant only in RLM soybean (Table 4) and the correlation between T_L and adaxial stomatal aperture was significant in both RLM and NRLM soybean. T_L did not show any significant correlation with either abaxial or adaxial stomatal aperture in cotton.

Similarly T_L showed significant and positive correlations with g_s (Table 4) and E (Table 4) in RLM and NRLM soybean at various times of the day. The coefficient of correlation was higher for RLM as compared with NRLM soybean. T_L had positive but statistically not-significant correlation with g_s and E in cotton.

Relationships among stomatal aperture, g_s and E: Abaxial stomatal aperture showed highly significant and positive correlations with g_s and E in both crops at various times of the day (Table 5). Adaxial stomatal aperture, however,

showed significant and highly significant positive correlations with g_s and E in cotton and RLM soybean, respectively (Table 5). Size of adaxial stomatal aperture showed significant positive correlation with E only in NRLM soybean. Stomatal conductance (g_s) was highly significantly positively correlated with E in both crops at various times of the day (Table 6).

Table 3: Stomatal conductance and transpiration rate of cotton and soybean in restrained (RLM) and not-restrained leaf movement (NRLM) in the morning (0900 h), noon (1200 h) and afternoon (1500 h)

Time (h)	Crop	St. Cond. (mol m ⁻² sec ⁻¹)	Transpiration (mmol m ⁻² sec ⁻¹)
0900 h	Soybean (NRLM)	0.50e	12.3e
	Soybean (RLM)	0.47e	12.2de
	Cotton	0.65b	15.0b
1200 h	Soybean (NRLM)	0.53d	13.7c
	Soybean (RLM)	0.61bc	15.3b
	Cotton	0.79a	17.6a
1500 h	Soybean (NRLM)	0.48e	11.7de
	Soybean (RLM)	0.49e	11.2e
	Cotton	0.56cd	13.8c

Means in the same category followed by different letters are significantly different at 5%

Table 4: Correlation of leaf temperature (TL) with stomatal aperture, stomatal conductance (g_s) and transpiration rate (E) of cotton and soybean in restrained (RLM) and Not-restrained Leaf Movement (NRLM)

Crop	Leaf Temp. (°C)	St. Aperture (μm)		St. Cond. (mol m ⁻² sec ⁻¹)	Transpiration (mmol m ⁻² sec ⁻¹)
		Abaxial	Adaxial		
Soybean (NRLM)		0.45	0.72*	0.66*	0.66*
Soybean (RLM)		0.79*	0.70*	0.88**	0.72*
Cotton		0.64	0.27	0.52	0.61

* Significant at p<0.05, ** Highly significant at p<0.001

Table 5: Correlation of abaxial and adaxial stomatal aperture with stomatal conductance (g_s) and transpiration rate (E) of cotton and soybean in restrained (RLM) and not-restrained leaf movement (NRLM)

Crop	1	2	3	4	5	6
Soybean (NRLM)		0.82**	0.93**		0.37	0.70*
Soybean (RLM)		0.95**	0.98**		0.88**	0.97**
Cotton		0.97**	0.99**		0.74*	0.75*

* Significant at p<0.05, ** Highly significant at p<0.001, 1- St. Aperture (μm) Abaxial 2- g_s (mol m⁻²sec⁻¹) 3- E (mol m⁻²sec⁻¹) 4- St. Aperture (μm) adaxial 5- g_s (mol m⁻²sec⁻¹) 6- E (mol m⁻²sec⁻¹)

Table 6: Correlation between stomatal conductance (g_s) and transpiration rate (E) of cotton and soybean in restrained (RLM) and not-restrained leaf movement (NRLM)

Crop	g_s (mol m ⁻² sec ⁻¹)	E (mmol m ⁻² sec ⁻¹)
Soybean (NRLM)		0.80**
Soybean (RLM)		0.93**
Cotton		0.99**

* Significant at p<0.05, ** Highly significant at p<0.001

DISCUSSION

Cotton showed higher FRSS, E and g, than soybean, which might be due to the frequently reported higher transpiration requirements of the crop (Wang *et al.*, 2004a, b). Significantly larger stomatal density and stomatal aperture (Kramer and Boyer, 1995) and the diaheliotropic leaf movement (Wang *et al.*, 2004b) might be responsible for higher transpiration in cotton. In RLM soybean; FRSS, the midday E, g, and T_L were higher than in NRLM soybean (Isoda *et al.*, 1994; Isoda and Wang, 2001). Larger transpiration in RLM soybean might be due to the larger increase in the size of abaxial stomatal aperture (Li *et al.*, 2004) and the leaf movement restraint (Isoda *et al.*, 1994; Isoda and Wang, 2001). Increase in the size of abaxial stomatal aperture might be an adaptive strategy of the RLM soybean in order to increase the E and thus keep the T_L low. The size of adaxial stomatal aperture didn't increase in restrained leaves, probably, because of the higher incident solar radiation which might have increased the loss of water from the guard cells of the adaxial stomata due to which the guard cells lost turgidity and the stomata did not open well. Higher T_L in RLM soybean despite the higher transpiration as compared with the NRLM is opposite to the frequently reported observation of transpirational cooling (Pettigrew, 2004). Its reason might be that when adaxial leaf surface, which is more solar radiation absorptive surface (Meyer and Walker, 1981), is exposed to solar radiation, it intercepts larger amount of solar radiation and thus its T_L increases. The RLM plants, as an adaptive strategy, might have increased transpiration to reduce T_L . Despite the higher transpiration rate, T_L of RLM soybean was higher than that of NRLM soybean, which shows that leaf movement was more effective in controlling/reducing T_L than the higher transpiration rate.

It was concluded that cotton increased its transpiration due to increase in the stomatal aperture and the diaheliotropism to keep its leaf temperature low at higher solar radiation. In soybean, on the other hand, the paraheliotropic leaf movement was more effective as compared with higher transpiration in controlling the leaf temperature.

REFERENCES

- Bressan, R.A., 2002. Stress Physiology. In Taiz L. and E. Zeiger Eds., Plant Physiology. 3rd Edn. Sinauer Associates, Inc. Sunderland, Massachusetts, pp: 591-623.
- Ehleringer, J.R. and Forseth, I.N. 1989. Diurnal Leaf Movements and Productivity in Canopies. In: Russel, G., B. Marshall and P.G. Jarvis (Eds.), Plant Canopies: Their Growth, Form and Function. Cambridge University Press, Cambridge, pp: 129-142.
- Fehr, W.R. and C.E. Caviness, 1977. Stages of soybean development. Iowa Agric. Home Econ. Exp. Stn., Iowa Coop. Ext. Serv. Spec. Rep, pp: 80.
- Hirose, T., T. Izuta, H. Miyake and T. Totsuka, 1992. A stomatal impression method using a fast-sticking adhesive. Jpn. J. Crop Sci., 61: 159-160.
- Inamullah and A. Isoda 2005. Adaptive responses of soybean and cotton to water stress II. CO_2 assimilation rate, chlorophyll fluorescence and photochemical reflectance index. Plant Prod. Sci., 8: 131-138.
- Isoda, A., T. Yoshimura and T. Ishikawa, 1994. Effect of leaf movement on radiation interception in field grown leguminous crops. III. Relation to leaf temperature and transpiration among soybean cultivars. Jpn. J. Crop Sci., 63: 657-663.
- Isoda, A. and P. Wang, 2001. Effects of leaf movement on leaf temperature, transpiration and radiation interception in soybean under water stress conditions. Tech. Bull. Fac. Hort. Chiba Univ., 55: 1-9
- Isoda, A. and P. Wang, 2002. Leaf temperature and transpiration of field-grown cotton and soybean under arid and humid conditions. Plant Prod. Sci., 5: 224-228.
- Kramer, P.J. and J.S. Boyer, 1995. Water relations of plants and soils. Academic Press, San Diego, pp: 201-256.
- Li, F., S. Kang and J. Zhang, 2004. Interactive effects of elevated CO_2 , nitrogen and drought on leaf area, stomatal conductance and evapotranspiration of wheat. Agric. Water Manage., 67: 221-233.
- Meyer, W.S. and S. Walker, 1981. Leaflet orientation in water stressed soybeans. Agron. J., 73: 1071-1074.
- Pettigrew, W.T., 2004. Physiological consequences of moisture deficit stress in cotton. Crop Sci., 44: 1265-1272.
- Sakuratani, T., 1981. A heat balance method for measuring water flux in the stem of intact plants. J. Agric. Meteorol., 37: 9-17.
- Wang, C., A. Isoda, Z. Li and P. Wang, 2004a. Growth and yield performance of some cotton cultivars in Xinjiang, China, an arid area with short growing period. J. Agron. Crop Sci., 190: 177-183.
- Wang, C., A. Isoda, Z. Li and P. Wang, 2004b. Transpiration and leaf movement of cotton cultivars grown in the field under arid conditions. Plant Prod. Sci., 7: 266-270.
- Wise, R.R., G.F. Sassenrath-Cole and R.G. Percy, 2000. A comparison of leaf anatomy in field-grown *Gossypium hirsutum* and *G. barbadense*. Ann. Bot., 86: 731-738.
- Wofford, T.J. and F.L. Allan, 1982. Variation in leaflet orientation among soybean cultivars. Crop Sci., 22: 999-1004.