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Effects of Leaf Movement on Radiation Interception in Field Grown Leguminous Crops

III. Relation to leaf temperature and transpiration among soybean cultivars*

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Abstract: Varietal differences of leaf movement in soybean were examined in terms of radiation interception, leaf temperature and transpiration. Five cultivars (c.v. Tsurukogane, Nanbushirome, Enrei, Tachinagaha and Miyagishirome) were grown under field conditions. An attempt was made to restrain leaf movement in the upper layers of the canopy with a nylon net. In the pod filling stage, intercepted radiation of each leaflet of two plants within the communities was measured by integrated solarimeter films for 2 days. Although intercepted radiation per unit ground area for each cultivar was not different between the control and the treatment, there was a large varietal difference in vertical distribution of mean intercepted radiation per unit leaf area. In the uppermost layer, Nanbushirome and Tsurukogane had larger values in the treatment, the other cultivars had smaller differences between the control and the treatment. A cultivar with smaller and thick leaflets tended to have larger intercepted radiation per unit leaf area. The effects of the treatment on leaf temperature and transpiration ability differed among the cultivars. Leaf temperature was regulated by the combination of leaf movement and transpiration. The magnitudes of these two factors might differ among the cultivars; leaf temperature was regulated mainly by leaf movement for Tsurukogane, Nanbushirome and Enrei and by both factors for Tachinagaha. Miyagishirome could not control leaf temperature in the day time on clear days, as compared to the other cultivars.
Key words: Intercepted radiation, Leaf movement, Leaf temperature, Soybean, Transpiration.

マメ科作物の葉の調位運動が受光量に及ぼす影響 第3報 ダイズ品種における葉温及び蒸散との関係：礒田昭弘・吉村登雄*・石川敏雄*・野島 博・高崎康夫(千葉大学園芸学部,*千葉大学映像隔測研究センター)
要　旨：ダイズの葉の調位運動の品種間差異について，受光量，葉温および蒸散速度の点から検討した．5品種（ツルコガネ，ナンブシロメ，エンレイ，タチナガハ，ミヤギシロメ）を圃場条件下で栽培し，登熟期に調位運動を抑えるため防雀網で群落上層を抑える処理を行った．群落内部の2個体の全小葉の受光量を簡易積算日射計で測定した．単位土地面積当りの受光量はいずれの品種も処理間に差はなかったが，単位葉面積当りの受光量は品種間差異があり，ナンブシロメ，ツルコガネの最上層では処理区の方が受光量が大きくなった．小葉面積が小さく，葉の厚い品種ほど単位葉面積当たりの受光量が大きい傾向があった．処理が葉温に及ぼす影響は品種間差異が大きく，ツルコガネ，ナンブシロメ，エンレイでは処理区の葉温が大きくなった．タチナガハ，ミヤギシロメでは処理間差は小さかった．無処理区の蒸散速度（単位葉面積当りの茎流速度）はタチナガハがもっとも大きく，エンレイが最小であった．葉温は葉の調位運動と蒸散によって制御され，これらの要因の係わり方は品種間で異なるものと考えられた．すなわち，ツルコガネ，ナンブシロメ，エンレイは主に調位運動によって，タチナガハは両者によって葉温が制御され，ミヤギシロメでは他品種に比べ葉温は余り制御できないものと考えられた．
キーワード：受光量，蒸散速度，ダイズ，調位運動，葉温．

Previously[7,8], we reported that the effectiveness of leaf movement for radiation interception under field conditions might depend on leaf area density in the upper layers of the canopy. This differed in peanut and soybean. Large varietal differences in leaf orientation were found in soybean[17]. However, detailed information to clarify the varietal differences of leaf movement under field conditions was lacking, particularly on the effect of radiation interception. Thus we examined the varietal differences in leaf movement in relation to radiation interception in plant communities to obtain information to depict the ideal type for

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radiation interception.

Paraheliotropic leaf movement would be related to the water conditions of the plants[1,2,11,12,15,16] and to the avoidance of excessive light and photoinhibition[6,10]. Leaf movement also regulates leaf temperature[8]. We also examined leaf temperature and water flow in the stem and analyzed the relationship between leaf movement, leaf temperature and transpiration.

Materials and Methods

Soybean was grown in the field of the experimental farm of the Faculty of Horticulture, Chiba University in 1992 and 1993. Five cultivars (Tsurukogane, Nanbushirome, Enrei, Tachinagaha and Miyagishirome) were used in both years. Tsurukogane is an indeterminate cultivar, grouped into Ib and became dwarfed and matured earlier in the Kanto area. The other four cultivars are the determinate type and grouped into IIc by Fukui and Arai's criterion of soybean ecotype classification in Japan[4]. The seeds were sown by hand at an equidistant spacing of 35 cm between and within rows on June 10 in both years. The seeding rate was one per stand. A combination of N, P_2O_5 and K_2O was applied in the ratio of 30, 100 and 100 kg ha^{-1} just before sowing.

Measurements of radiation interception were made on August 14 and 15 in 1992, at the young pod stage. Two plants with equal leaf numbers were selected from the center of the plot. Integrated solarimeter films[18] were stuck on every leaflet surface by double-sided binding tapes for two days as described previously[8]. In the treated plants, the surfaces of the canopy of 10 plants, including the two sample plants were covered twice, with a 0.56 mesh nylon net. Consequently, leaves in about a 10 cm layer from the surface of the canopy, were restrained horizontally. At the same time, vertical distribution of leaf area, leaf, stem and pod weights of four plants per cultivar were examined at 10 cm intervals.

Leaf and air temperatures were measured in both the control and treated plants by thermopiles from 4 : 00 h to 19 : 00 h on August 14 in 1992. Terminal leaflets were selected from the uppermost part of the canopy. The details of the measurement were the same as reported in the previous paper[8]. For Nanbushirome, the data obtained in 1991 were used, since the 1992 data was incomplete. Water flow in stem of the plant in the control was measured by sap flow gauges (Dynamax Inc., Dynagage) on August 31 in 1993. The sap flow gauges were attached to the base of the main stem. The data of the sap flow gauges were collected at one minute intervals by a data logger (Eto Denki Corp., Thermodac E) connected to a personal computer.

Results

1. Intercepted radiation

The leaf number was a little different between the control and the treatment ; the leaf area index (LAI) of the treatment was smaller for Tsurukogane, Enrei and Tachinagaha but larger for Miyagishirome (Table 1). The LAIs were smaller in Tsurukogane and largest in Miyagishirome. Conversely, mean intercepted radiation per unit leaf area was largest in Tsurukogane and smallest in Miyagishirome. The values of the other cultivars were around 4.5 MJ m^{-2} day^{-1}. This indicates that a cultivar with a small LAI intercepted larger amount of radiation per unit leaf area. There was no significant difference in intercepted radiation per unit leaf area between the control and the treatment for all the cultivars ($P=0.50$ level). Intercepted radiation per unit ground area did not also differ between the control and the treatment. This is on the assumption that, the leaf area of the control and the treatment was similar. Tsurukogane intercepted a larger amount of radiation though it had the smallest LAI. On the contrary, Miyagishirome with the largest LAIs intercepted the lowest amount of solar radiation.

Fig. 1 indicates vertical distribution of mean intercepted radiation per unit leaf area. Tsurukogane had the largest values in every layer, as compared to the other cultivars. The values of Miyagishirome were the smallest. Tsurukogane and Nanbushirome generally had higher values in each layer of the treated plants, especially in their uppermost layer. On the contrary, Enrei, Tachinagaha and Miyagishirome tended to have smaller values in the treatment. In the uppermost layer, the values of the control and the treatment were not different in Tachinagaha and Miyagishirome. Although only Enrei had a higher value in the control, it represented the mean value of only

Table 1. Leaflet number, leaf area index and intercepted radiation.

Cultivar	Leaflet number (plant^{-1})		Leaf area index (m^2 m^{-2})		Mean intercepted radiation per unit leaf area (MJ m^{-2} days^{-1})				Total intercepted rediation per unit ground area (MJ m^{-2} day^{-1})	
					Mean		S.D.			
	C	T	C	T	C	T	C	T	C	T
Tsurukogane	118	88	2.21	1.88	6.06	6.31	4.52	4.38	15.7	12.9(15.2)*
Nanbushirome	115	128	2.77	2.65	4.66	4.66	2.89	3.45	15.1	15.4(16.1)
Enrei	90	72	2.88	2.57	4.45	4.58	2.86	3.85	15.1	14.4(16.1)
Tachinagaha	85	72	2.94	2.74	4.85	4.81	3.59	3.62	17.3	16.0(17.2)
Miyagishirome	109	113	3.87	4.37	2.81	2.83	2.58	3.16	13.4	15.5(13.7)

C : Cotrol, T : Treatment (restraint of leaf movement).
* : Assumed value when leaf areas of the control and the treatment are similar.

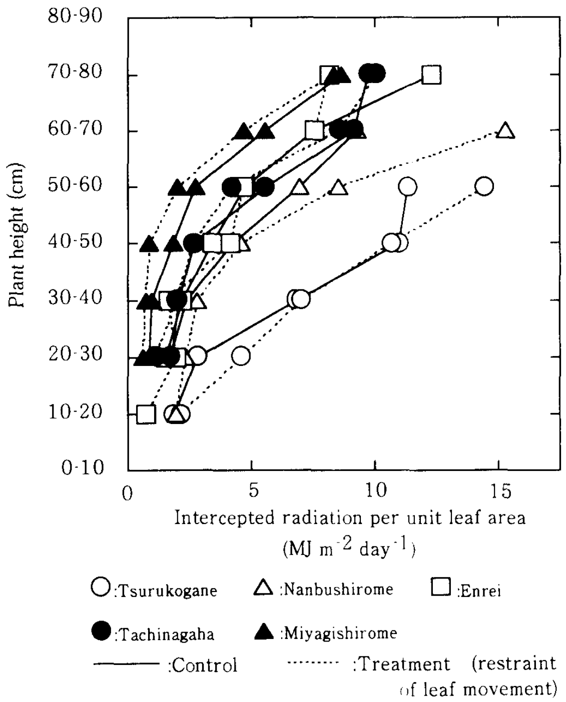

Fig. 1. Vertical distribution of mean intercepted radiation per unit leaf area.

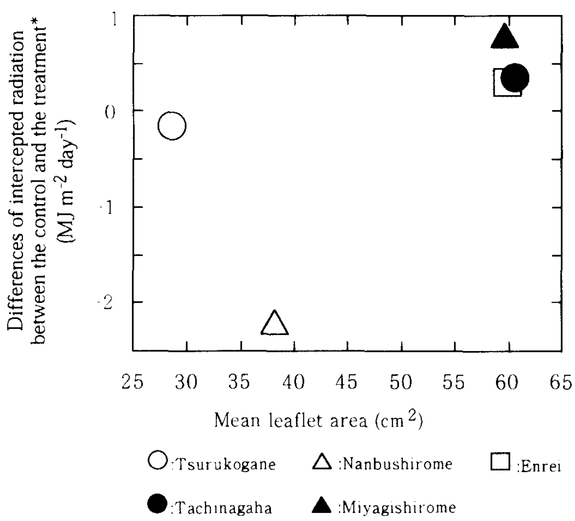

Fig. 2. Relationship between mean leaflet area and difference of intercepted radiation between the control and treatment (restraint of leaf movement) in the upper two layers.
*a negative value is an indication of the treated plant intercepting larger amount of radiation than the control.

three leaflets of the uppermost layer of the control. There was a tendency for a cultivar with a smaller leaflet area to intercept a larger amount of radiation.

Fig. 2. shows the relationship between the leaflet area and the differences in intercepted radiation between the control and the treatment in the upper two layers (a negative value indicates that the treated plants intercepted a larger amount of radiation as compared to the control). In Tsurukogane, a large difference between the control and the treatment was not observed. It was presumed that, the restraining treatment of the upper leaves of the canopy could not affect radiation interception. This is because of the smaller leaf concentration in the upper layers. Enrei, Tachinagaha and Miyagishirome, which had larger leaflet areas, had positive values. Mutual shading would be made more severe by treatment in the upper layers because of their larger leaflet areas. On the contrary, Nanbushirome showed a high negative value, indicating that unintercepted radiation would be reduced by the tilting up of the upper leaves due to the restraining.

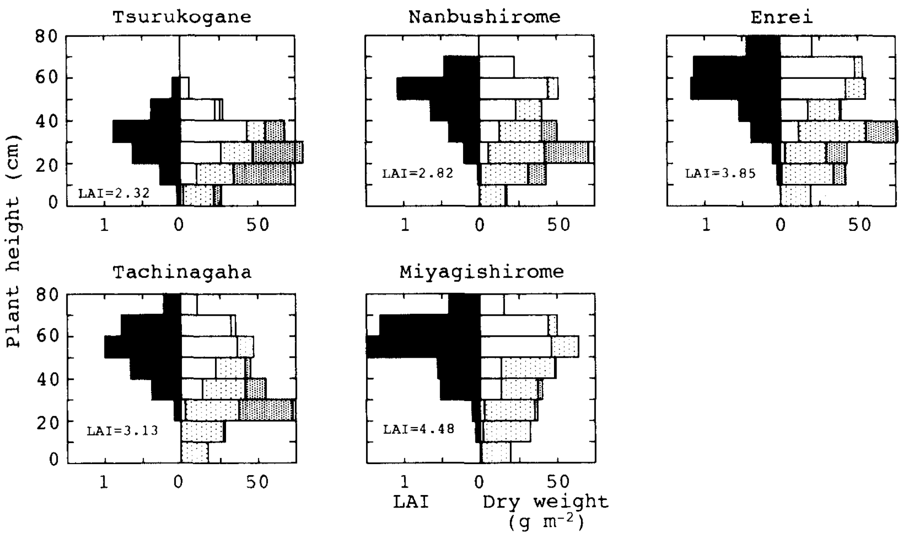

Fig. 3. Vertical distribution of leaf area index (LAI) and dry weights.

2. Canopy structure and specific leaf area

Tsurukogane and Nanbushirome showed a round canopy type which had the highest LAI in the middle layer, with a small LAI and low plant height (Fig. 3). Tachinagaha also had rather large LAIs in the middle layers but higher plant height. Enrei and Miyagishirome showed the table type which had large LAIs in the upper layers of the canopy. In particular, LAIs of the upper layers were large in Miyagishirome.

Fig. 4 indicates vertical distribution of specific leaf area (SLA). All the cultivars tended to have lower values towards the top of the canopy. Tsurukogane had the smallest value in each layer followed by Nanbushirome, Tachinagaha and Enrei. Miyagishirome had the largest SLA in most layers, indicating large and thin leaves.

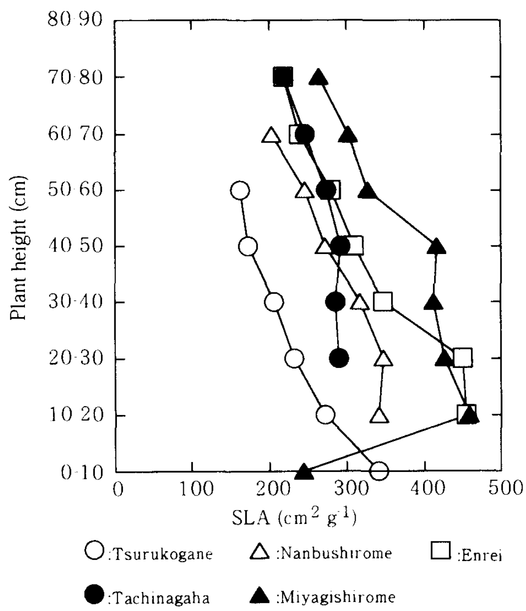

Fig. 4. Vertical distribution of specific leaf area (SLA).

3. Leaf temperature and water flow in stem

Leaf temperatures of Tsurukogane, Nanbushirome and Enrei were higher in the treatment during day time as compared to the control (Fig. 5). The leaf temperature of the control was at par with air temperature, though those in Tsurukogane and Enrei were a little higher than the air temperature. In Tachinagaha, the temperature of the treated plant was not so high as that of the control, which had a similar change to that of air temperature. On the other hand, the temperatures of both the control and treatment in Miyagishirome were higher than air temperature. The changes in the temperature of the control were similar to those of the treatment.

The data of the water flow in the stem per unit leaf area were taken during the period from 12 : 00 h to 13 : 00 h because this period showed a marked difference (Fig. 6). There were greater differences in transpiration ability among the cultivars. The water flow per unit leaf area was the lowest for Enrei during the experimental period and did not fluctuate so

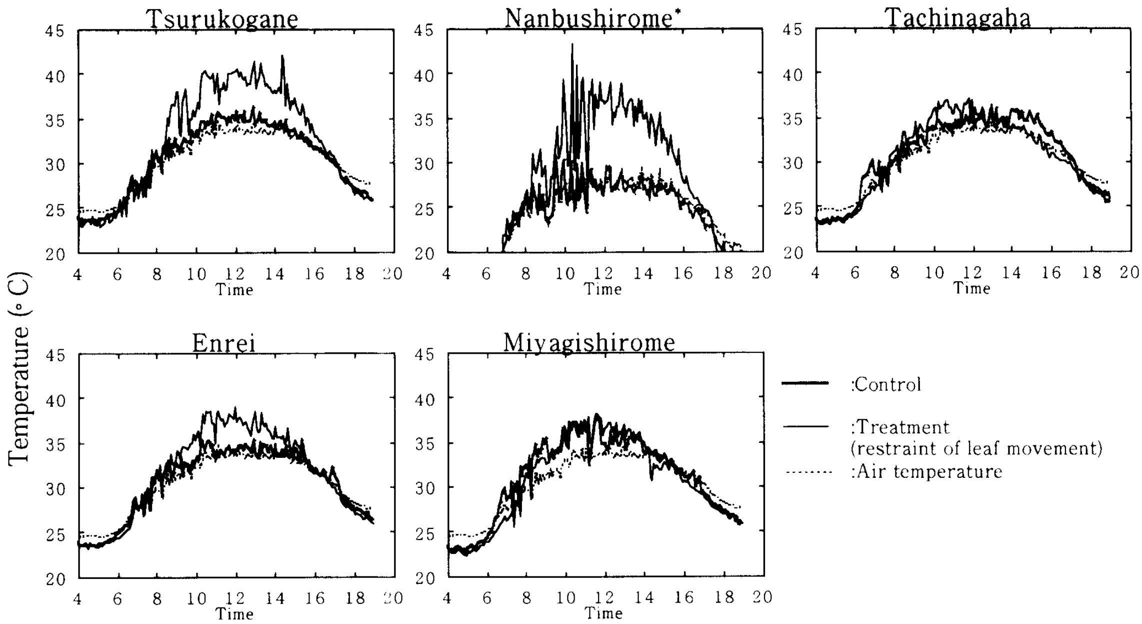

Fig. 5. Changes in the leaf temperatures of the control and treatment on August 28 with time.
*The data of August 14 in 1991 were used for Nanbushirome.

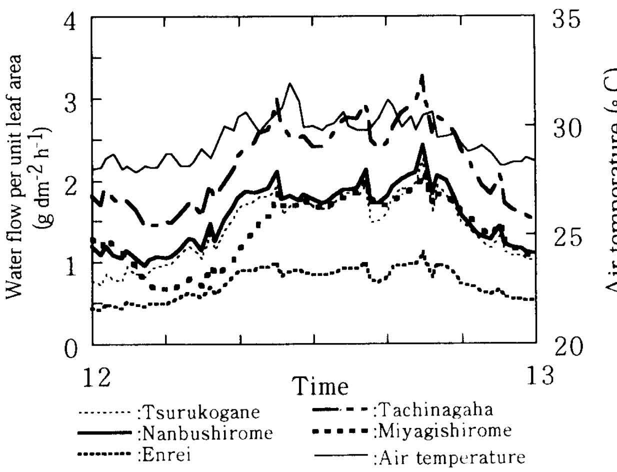

Fig. 6. Changes in water flow in the stem per unit leaf area with time.

largely. Tachinagaha had the highest values followed by Nanbushirome, Miyagishirome and Tsurukogane. The maximum value was about three times that of Enrei at 12 : 47 h.

Discussion

There were differences in intercepted radiation per unit leaf area among the cultivars as summarized in Table 2. Tsurukogane and Nanbushirome generally had higher values in each layer of the treated plants as compared to the control. This is an indication of active leaf movement (paraheliotropic). On the other hand, Enrei, Tachinagaha and Miyagishirome tended to have smaller values in the treatment. Basically, cultivars with smaller and thicker leaflets tended to move leaves drastically, as in Tsurukogane and Nanbushirome. In Chinese cultivars, however, a cultivar with large leaflets and active leaf movement has been identified[16]. Other factors besides leaf size and thickness may also be associated with the activity of the leaf movement, such as movement of ions in pulvinule cells[14].

There was no marked difference in intercepted radiation per unit ground area between the control and the treatment in all the cultivars. This effect, which increased total intercepted radiation by the tilting up of the upper leaves as in peanut[7], was not observed in this study. In Tsurukogane and Nanbushirome, the restraining treatment was not effective because of their sparse leaf area in the upper layers of the canopy, although their leaf movement was active. Tachinagaha also did not have dense leaf area in the upper layers and Enrei had less active leaf movement as compared to Tsurukogane and Nanbushirome. There was inactive leaf orientation in Miyagishirome because of its larger and thin leaves, in spite of having large LAIs in the upper layers. Thus the effectiveness of leaf movement (paraheliotropic) in increasing

Table 2. Summary of features observed in the experiment.

Cultivar	Intercepted radiation per unit leaf area	Difference in intercepted radiation*	Difference in leaf temperature	Leaf area index	Leaflet area	Specific leaf area	Transpiration	Leaf movement
Tsurukogane	High	No	Large	Small	Small	Small	Medium	Active
Nanbushirome	Medium	−Large**	No	Medium	Small	Small	Medium	Active
Enrei	Medium	+Small**	Large	Medium	Large	Medium	Low	Medium
Tachinagaha	Medium	+Small**	Small	Medium	Large	Medium	High	Medium
Miyagishirome	Low	+Small**	Small	Large	Large	Large	Medium	Inactive

* The upper 2 layers.

** +and− indicate that the value in the control was larger or smaller than that in the treatment, respectively.

intercepted radiation is advantageous only under conditions of severe mutual shading in the upper layers of the canopy. We reported a canopy structure with smaller leaflets and sparse leaf area in the upper layers is advantageous for radiation penetration[9] as in the case of this experiment. In terms of radiation interception and utilization, a cultivar with smaller leaflets and active leaf movement is advantageous under high planting density. For further discussion, other experiments using cultivars with smaller leaflets and active leaf movement under high density is needed.

Hirata et al[6] and Kao and Forseth[10] reported that the heliotropic leaf orientation modulates incident light to maximize photosynthesis. This orientation minimizes the risk of damage to the photosynthetic apparatus due to environmental stress. In particular, several reports have related the leaf angle and irradiance to leaf water potentials[1,10,11]. On the other hand, Sato[13] reported that the changes in the twisting angle of the lateral leaflets seemed to be associated with leaf temperatures, not with leaf water potentials. In this experiment, the leaf movement was also found to regulate the leaf temperature as previously reported[8] and varietal differences in transpiration rates were also observed. The transpiration rate was associated with the regulation of leaf temperature[5]. Thus leaf temperature would be regulated by the combination of leaf movement and transpiration, according to Table 2. The magnitudes of the two factors differ among the cultivars, i.e. Tsurukogane and Nanbushirome regulate leaf temperature mainly by leaf movement. Leaf temperature in Enrei also may be controlled by leaf movement not by its lowest transpiration rate. Both leaf movement and transpiration in Tachinagaha would be related to the leaf temperature. Miyagishirome with large and thin leaflets could not control the leaf temperature in day time on clear days, due to its lower transpiration rate and inactive leaf movement.

Leaf movement has two reversible aspects, paraheliotropic and diaheliotropic movements[1,15]. Every species has different leaf orientation aspects and the leaf movement is more adapted to the environmental conditions[3]. In soybean, the leaf movement in most of day time is the paraheliotropic movement, even under non-water stress conditions. Besides photoinhibition, paraheliotropic leaf movement may reduce mutual shading and increase intercepted radiation in the canopy with higher LAIs as mentioned above. In addition, there is another possibility that a cultivar with high transpiration ability will delay the transition from the diaheliotropic to paraheliotropic movement and increase intercepted radiation by the extension of the phase of diaheliotropic leaf movement.

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