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Growth and Adaptation of Soybean Cultivars under Water Stress Conditions

II. Effects of leaf movement on radiation interception*

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Abstract : Leaf movement of field-grown soybeans under water stress conditions was examined with radiation interception. Two cultivars with different leaf movement, Zhenzhuta 2 (active) and Heinong 33 (inactive), were grown in concrete plots in Xingjiang, China. At the pod filling stage, the plants were subjected to four different levels of irrigation. Intercepted radiation of every leaflet of two plants in each plot was measured by integrated solarimeter films for 2 days. There were large varietal differences in leaf movement affecting radiation interception. The upper leaves of Zhenzhuta 2 tended to intercept greater amount of radiation and the efficiency of radiation interception against leaf area was higher, as the amount of irrigation increased, indicating that paraheliotropism in the morning was inactive due to the water supply. Heinong 33 did not differ in radiation interception among the treatments except in the severest water stress plot. Radiation in the severest water stress plot penetrated less because of the wilting of the leaves during the day time. Paraheliotropic movement in Zhenzhuta 2 became inactive in the morning, after the temporary irrigation following the water stress treatments. Heinong 33 recovered from wilting and moved its leaves paraheliotropically during the day time.
Key words : Drought resistance, Integrated solarimeter film, Irrigation treatment, Leaf movement, Radiation interception, Soybean, Water stress.

乾燥条件下におけるダイズの生育と適応　第2報　葉の調位運動が受光量に及ぼす影響：王　培武・礒田昭弘・魏　国治**・吉村登雄***・石川敏雄***（千葉大学園芸学部・**中国石河子農学院・***千葉大学映像隔測研究センター）

要　旨：水分ストレス条件下でのダイズの葉の調位運動が小葉の受光量に及ぼす影響を検討するため，中国新疆ウイグル自治区石河子のコンクリート枠圃場で実験を行った．調位運動の活発な珍珠塔2号と不活発な黒農33号を用い，登熟期に4段階のかん水処理区を設け，38日間処理を行った．処理期間中に各区より2個体を選び，その全小葉の2日間の受光量を測定した．また，処理終了2日後に一時的にかん水を行い群落内相対照度を測定した．両品種の葉の調位運動には大きな差異があり，受光量も異なった．珍珠塔2号の上層葉は，かん水量が増えるにしたがい強い光を受光する葉が多くなり，午前中太陽光線に対する平行運動(Paraheliotropic movement)が小さくなった．黒農33号では，処理間差はあまり大きくなかったが，最も水分ストレスが強かった区では昼間葉の萎れ現象がみられ，光の透過が悪化した．最も水分ストレスの強かった区で，処理終了後の一時的かん水により珍珠塔2号では午前中，太陽光線に対する平行運動が小さくなることが認められた．黒農33号では萎れ現象は回復したものの，平行運動を続けていた．
キーワード：簡易積算日射計，かん水処理，受光量，水分ストレス，耐旱性，ダイズ，調位運動．

It is known that two types of leaf movement exist, diaheliotropism and paraheliotropism[6,18] and that these movements may be modified by water availability[12,14,15,16]. In the previous paper[19], leaf movement and its effect on leaf temperature of soybean was investigated under irrigated and non-irrigated conditions. There were large varietal differences in leaf movement and leaf temperature with regard to active and inactive leaf movement cultivars. This indicates that paraheliotropic leaf movement has the role of avoiding the increase in leaf temperature under water stress conditions. Leaf movement also affects radiation interception, which is concerned with dry matter porduction, i.e. paraheliotropic leaf movement decreased intercepted radiation in sparse pop-

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Table 1. Amount of irrigation during the experiment (mm).

Treatment	Date								Total	Precipitation
	June		July							
	20	25	2	6	9	14	18	25		
I	0	20.8	0	0	0	0	0	0	20.8	22.8
II	36.5	15.0	4.1	4.1	15.0	15.0	15.0	15.0	119.7	22.8
III	52.4	20.8	7.4	7.4	30.1	30.1	30.1	30.1	208.4	22.8
IV	66.6	30.1	15.1	15.1	45.1	45.1	45.1	45.1	307.4	22.8

Table 2. Leaf number, leaf area index (LAI) and intercepted radiation.

Treatment	Leaflet number (plant^{-1})		LAI (m^2m^{-2})		Intercepted radiation per unit leaf area (MJ $m^{-2}day^{-1}$)		Intercepted radiation per unit ground area (MJ $m^{-2}day^{-1}$)	
	Zhengzhuta 2	Heinong 33	Zhengzhuta 2	Heinong 33	Zhengzhuta 2	Heinong 33	Zhengzhuta 2	Heinong 33
I	70	117	2.85	2.14	2.61(1.82)	3.80(2.16)	17.09	18.13
II	74	130	2.54	3.72	3.07(2.15)	2.88(2.60)	18.94	23.24
III	76	89	2.57	2.37	4.29(3.46)	4.15(3.52)	26.25	22.28
IV	71	103	3.15	2.93	3.29(3.84)	3.46(3.01)	24.35	22.85

( ) : Standard deviation.

ulation ; and reduced severe mutual shading effects in dense leaf area distribution[9]. In this experiment, we intended to investigate the effects of leaf movement on radiation interception as water deficit increases.

Materials and Methods

The experiment was conducted at the experimental farm of Shihezi Agriculture College, Xingjiang, China in 1990. The field consists of four concrete framed fields (3.6 m × 32 m with 1.8 m in depth). Two cultivars, Zhengzhuta 2 (active leaf movement and short stature) and Heinong 33 (inactive leaf movement and long stature), were sown at equidistant spacings of 35 cm on April 26. The seeding rate was 2 or 3 per hill, which was thinned to one per hill after emergence. The other conditions of the cultivation were as in the previous paper[19]. Four levels of irrigation treatments were conducted as shown in Table 1 (from June 20 to July 28). After the treatment, temporary irrigation (45.1 mm) was made in Treatment IV on July 28.

The measurement of radiation interception was done on July 7 and 8 (17 days after the treatment). Two plants of each cultivar were selected from the center of the plot in terms of equal leaf numbers. Integrated solarimeter films[20] were stuck on every leaflet surface by double-sided binding tapes for two days. The details of the measurement were the same as reported by Isoda et al. [7]. The experimental days were clear ; and the global solar radiation for the two days was 14.3 MJ m^{-2} day^{-1}.

On July 30 (the 2nd day after the temporary irrigation), vertical distribution of leaf area, leaf, stem and pod weights of four plants of each cultivar were exmined at 10 cm height intervals. At the same time, relative light intensities were also measured at 30 points per 10 cm of plant height around 7 : 00 h, 12 : 00 h, and 19 : 00 h using a relative light intensity photometer (Sanshin Kogyo Corp., NS-2).

Results

1. Leaf number and mean intercepted radiation

Table 2 shows leaflet number, leaf area index (LAI) and intercepted radiation per unit leaf area and per unit ground area. Treatment III had the largest mean intercepted radiation per unit leaf in both cultivars. The values of Treatments I and II were the smallest for Zhengzhuta 2 and Heinong 33, respectively. The value of Treatment I in Heinong 33 was higher, suggesting that its leaves intercepted radiation rather perpendic-

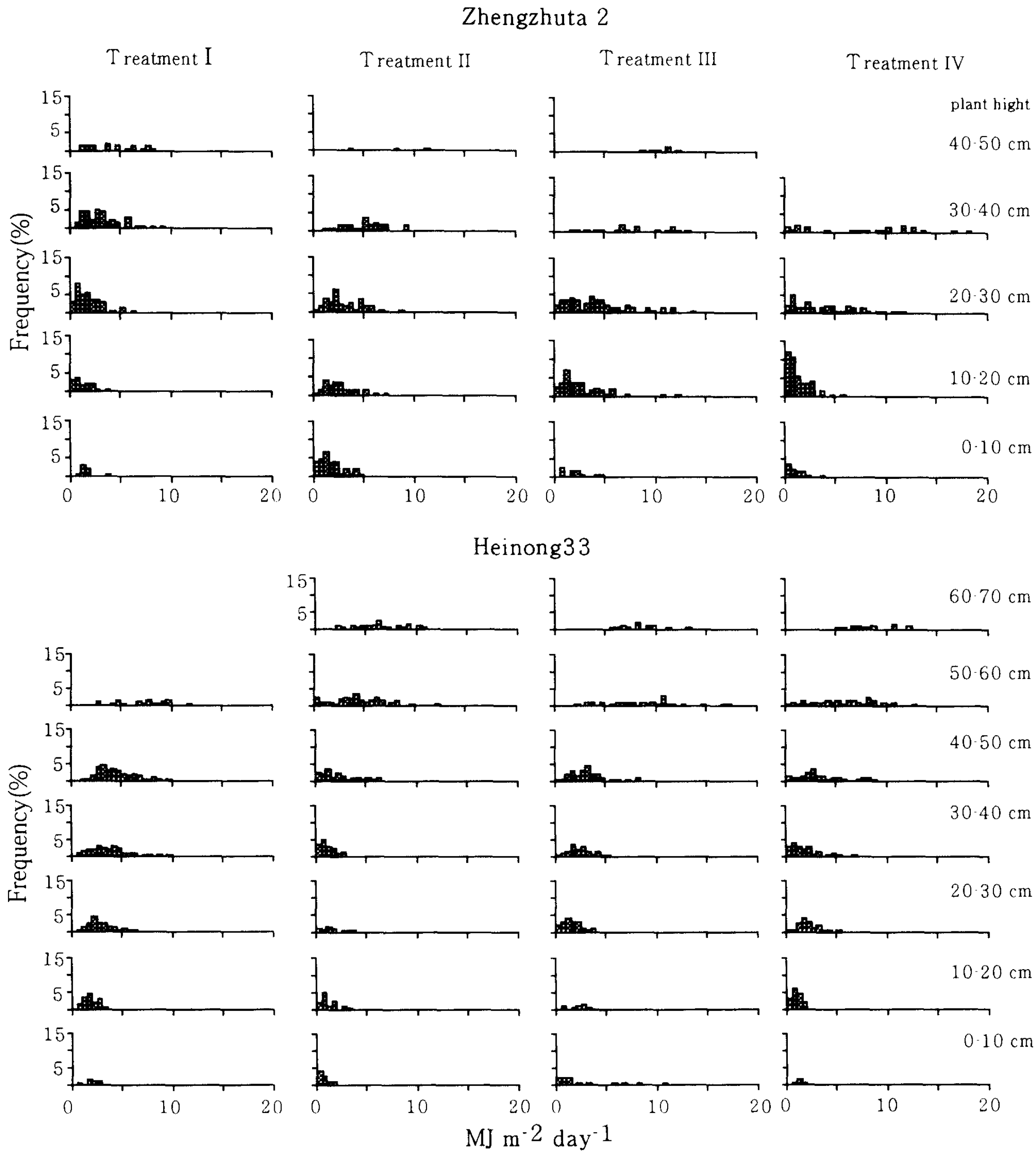

Fig. 1. Frequency distribution of intercepted radiation per unit leaflet area with plant height.

ularly because of the wilting of the leaves during the day time. Intercepted radiation per unit ground area tended to increase with the amount of irrigation in both cultivars, although Treatments III and IV of Zhenzhuta 2 were similar and Treatment II of Heinong 33 was the highest.

2. **Frequency distribution of intercepted radiation**

Frequency distribution of intercepted radiation per unit leaf area differed between the cultivars and among the treatments (Fig. 1). In the upper two layers of Zhenzhuta 2, a well-irrigated plot tended to intercept the larger value of radiation. In particular, the total accumulated value of Treatment IV was almost 20 MJ m^{-2} day^{-1}, which was greater than global solar radiation. Heinong 33 showed little difference among the treatments, although there were several leaflets which intercepted larger radiation in the upper two layers of Treatments III and IV as compared to Treatments I and II. The maximum value was recorded in the second layer of Treatment III.

3. **Canopy structure and the amount of intercepted radiation**

Fig. 2 shows vertical distribution of interce-

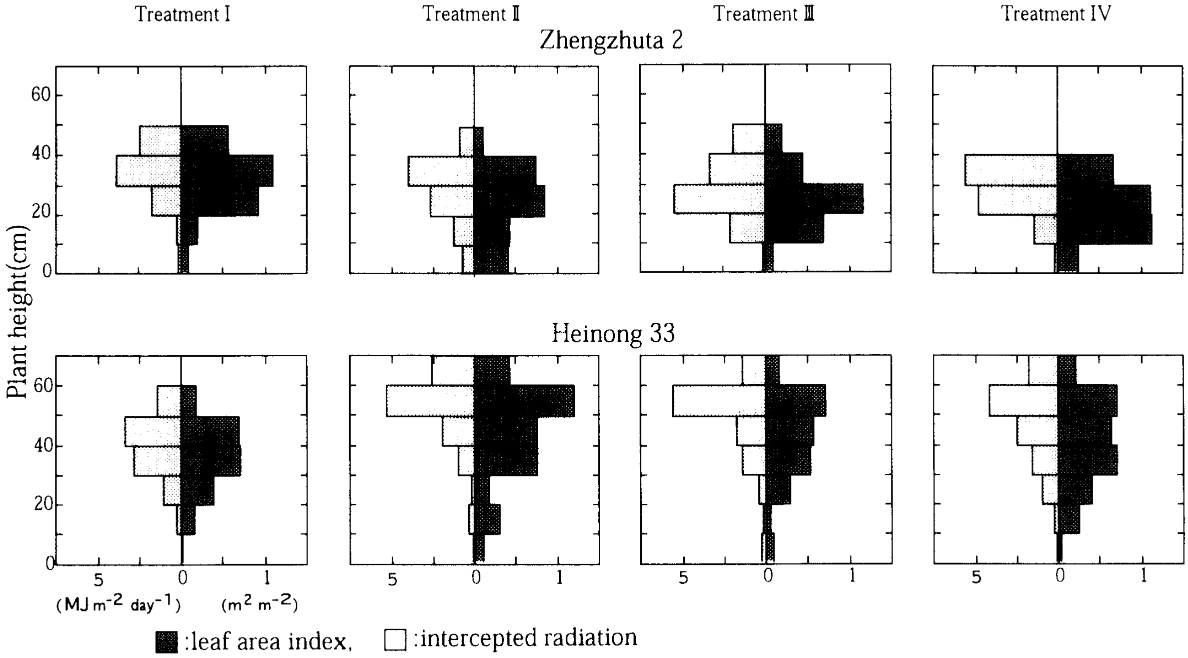

Fig. 2. Vertical distribution of intercepted radiation and the leaf area index within canopies.

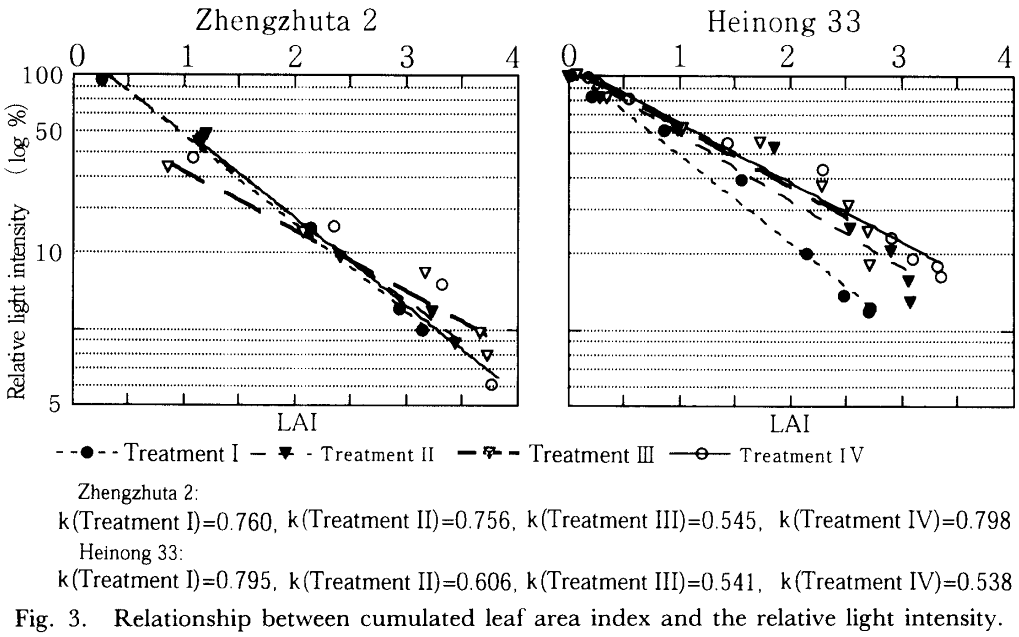

Fig. 3. Relationship between cumulated leaf area index and the relative light intensity.

pted radiation and leaf area index (LAI) within the canopies. Zhengzhuta 2 had different distribution of intercepted radiation and LAIs among the treatments. Treatment I and II had the largest LAI in the middle layer of the canopy and the lower layers were the largest in Treatment III and IV. The upper layers tended to have larger amount of radiation, except Treatment III. The upper layer of a well-irrigated plot tended to intercept larger amount of radiation per unit leaf area. Treatment IV intercepted larger amount of radiation in the upper two layers as compared to Treatments I and II, indicating less paraheliotropic leaf movement. In Heinong 33, distribution patterns of intercepted raidation and LAIs were not so different among the treatments as compared to Zhengzhuta 2, although the total amount of intercepted radiation in Treatment I was smaller.

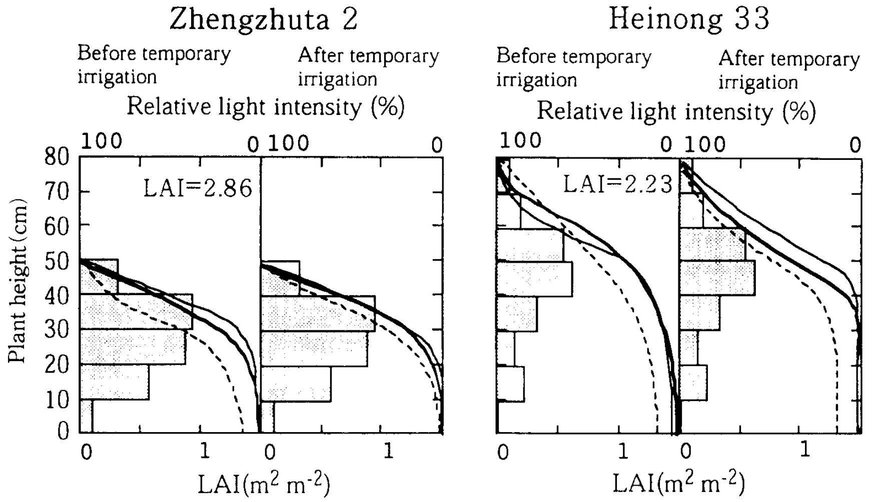

Fig. 4. Relative light intensity within the canopy before and after temporary irrigation in Treatment I.

The second layer from the top intercepted the greatest amount of radiation and intercepted radiation was small towards the base of the canopy.

4. Relationship between LAI and relative light intensity

Fig. 3 shows the relationship between cumulated LAI and relative light intensity with plant height on July 9. The inclinations (light extinction coefficient, k) of Zhengzhuta 2 did not differ among the treatments, except in Treatment III. The k value of Treatment III was smallest, indicating that more radiation was intercepted. Heinong 33, except in Treatment I, had smaller k values than Zhengzhuta 2 due to its taller plant height and sparse leaf area distribution. Treatment I showed a higher k value (0.795) and the light penetration was worse because the wilting of leaves progressed during the day time.

5. Effects of temporary irrigation

At noon, solar radiation generally penetrated deeper as compared to that of the early morning and the late evening (Fig. 4). Radiation penetration within the canopy changed in Treatment I of Zhengzhuta 2 before and after temporary irrigation. Before temporary irrigation, radiation at noon penetrated deeper into the canopy as compared to that in the early morning and the late afternoon, indicating that the greater amount of radiation was permeated by paraheliotropic leaf movement. After temporary irrigation, however, paraheliotropic movement during the day time became inactive and the difference among measuring periods was less than that before irrigation. The leaves responded immediately to adequate water conditions and intercepted more radiation. On the other hand, the leaves of the upper layers in Heinong 33, were wilting during the day time and recovered from wilting in the late afternoon under water stress conditions. The radiation at noon was intercepted by the uppermost wilting leaves. After temporary irrigation, the upper leaves recovered from wilting and moved paraheliotropically during the day time. This resulted in the increase of unintercepted radiation as compared to Zhengzhuta 2.

Discussion

Several reports have cited that paraheliotropic leaf movement increased as leaf water potential decreases[1,11,15,18]. Although leaf water potential was not measured in this experiment, it was found that leaf movement, including paraheliotropism and diaheliotropism, was related to the amount of irrigation. Previously, we reported that the leaf temperature of the irrigated plot in Zhengzhuta 2 was higher than air temperature during the morning, suggesting that the leaves moved diaheliotropically[19]. On the other hand, the leaf temperature of the non-irrigated plot was at par with air temperature, exhibiting paraheliotropic leaf movement. The results of intercepted radiation obtained in this experiment coincided with the changes of the leaf temperatures. Intercepted radiation in Zhengzhuta 2 tended to increase as the amount of irrigation was increased, though Treatment III was the highest. These results indicate that the increase of water availability extended the period of diaheliotropic leaf movement and there would be an optimum amount of irrigation for intercepted radiation. Therefore, proper water management may increase intercepted radiation in the irrigated culture of soybean, and subsequently, increase of dry matter production.

After temporary irrigation following the water stress period, paraheliotropism in Zhengzhuta 2 became inactive, although the changes in leaf temperature showed a certain degree of persistency of paraheliotropic rhythm[19]. On the other hand, Heinong 33 showed no increase of intercepted radiation after the temporary irrigation. This result suggests large varietal differences in physiological responses to water deficit. There are several reports about physiological factors that relate to drought resistance of soybean, i.e. water potentials, photosynthetic rate, stomatal resistance[2-5,10,21]. Besides these physiological factors, leaf movement may also be one of the functions of drought resistance and adaptation, such as paraheliotropism as an avoidance of excessive-light damage mechanism ; and inactive paraheliotropism after the cessation of water stress. Sammons et al. [17] reported that varietal differences in the yield of Medrski and Jeffers' field study[13] were not entirely consistent with the differences in the data on seedling performance, including water potentials and photosynthetic rate. In addition to the differences in maturation ; and between population and individuals, the inconsistency between these data might be related to population performance, including the effects of leaf movement as discussed above. Paraheliotropic leaf movement has the role of avoiding the increase of leaf temperature under water stress conditions[19]. Isoda et al. [8] reported that leaf temperature may be controlled by transpiration and paraheliotropic leaf movement ; and the magnitudes of these two factors may differ among the cultivars, suggesting that leaf movement would be one of the mechanisms for adaptation under drought and/or high light conditions. If the relation of leaf movement to dry matter production is investigated further, leaf movement may be used as a criterion of drought resistance under field conditions.

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