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Effects of Pre-Flowering Soil Moisture Deficits on Dry Matter Production and Ecophysiological Characteristics in Soybean Plants under Drought Conditions during Grain Filling*

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Abstract : Summer crop plants grown in rain-fed fields suffer from drought during a hot and relatively dry summer after the rainy season called "Baiu" in Japan. Since crop plants might develop vigorous shoots with poorly developed root systems during the rainy season, they might suffer from water deficits in the summer, even when soil moisture depletes on the surface of the soil. In order to confirm this, the effects of pre-flowering soil moisture deficits on dry matter production and ecophysiological characteristics thereafter were investigated in soybean plants.

Under deficient soil moisture conditions after flowering, higher dry matter production and higher grain yield were attained in the plants grown under deficient soil moisture before flowering (D-plot) than in the plants grown under sufficient soil moisture (W-plot). Large net assimilation rate (NAR) was responsible for high dry matter production in the plants of the D-plot. High NAR in the plants of the D-plot resulted from (1) a root system that was well developed in deep soil layers, (2) their capacity to absorb much soil water, especially in deep soil layers, (3) maintenance of a high leaf water potential and, therefore, a high photosynthetic rate during daytime and (4) a delay in the decrease in photosynthetic rate due to senescence. It was concluded that improved cultivation for developing root systems, such as drainage in the rainy season, as well as irrigation in midsummer, will be important in the cultivation of field summer crop plants in Japan.
Key words : Dry matter production, Photosynthesis, Root system development, Senescence, Soil moisture, Soybean, Water deficits, Water uptake.

開花前の低土壌水分が稔実期の乾燥条件におけるダイズの乾物生産と生理生態的性質に及ぼす影響 :
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要　旨 : わが国の夏作物の生育期間には，梅雨と盛夏の比較的乾燥する時期がある．乾燥地や半乾燥地に比較すれば乾燥する時期でも土壌水分の減少ははるかに少ないが，この期間に夏畑作物は干ばつ害を受けることがある．夏畑作物は栄養生長の盛んな時を梅雨期の土壌水分が多く湿度の高い条件で過ごすので，茎葉は大きく繁茂し，根は浅くはり根系の発達は劣る．このような作物は梅雨後の夏の比較的乾燥する条件におかれると，表層土壌の水分が減少しただけで水ストレスを受ける，いいかえると，梅雨期の多雨多湿条件が夏畑作物の水ストレスを助長していると考えられる．

この考えを検討する試みとして，ダイズを用いて開花期まで湿潤土壌（湿潤区）と低水分土壌（乾燥区）の圃場に生育させた後，両区とも稔実期を低水分土壌で生育させ，乾物生産とこれに関係する生理生態的性質を比較した．その結果，乾燥区のダイズは湿潤区に比較して稔実期の純同化率 (NAR) が高いことによって乾物生産を高く維持し，子実生産も高くなった．乾燥区のダイズの NAR が高くなったのは，(1) 土壌の深くまでよく発達している根系をもち，(2) 土壌の深い部分から水分を多く吸収でき，その結果，(3) 日中の葉の水ポテンシャルを高く維持し，光合成速度の日中低下が小さく，そして (4) 老化に伴う光合成速度の減少が小さい，などによるものであった．本研究により，わが国の夏畑作物の栽培においては夏のかんがいだけでなく，梅雨期の排水などによって根系をよく発達させることが重要であることが指摘できた．
キーワード : 乾物生産，吸水，光合成，根系の発達，水分欠乏，ダイズ，土壌水分，老化．

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Japan is located in the Asian monsoon climate region. Annual precipitation, which is more than 1,500 mm in many regions of Japan, exceeds annual evaporation. However, rainfall isn't distributed uniformly throughout the year. During the growing seasons of summer crops, there is a period of midsummer, between the rainy season called "Baiu" from the middle of June to the middle of July and the typhoon season of September and October (Fig. 1). Atmospheric moisture conditions change greatly and rapidly after "Baiu". Evaporation exceeds precipitation significantly during the midsummer (Fig. 1). Crop plants grown in rain-fed regions suffer from drought during this period, especially when there is little rainfall. Therefore, many irrigation systems have been equipped in the field as well as in the paddy field[20].

It had been observed in groundnut plants that the more precipitation there is during midsummer, the higher the yield. However, it had been observed as an exception that the plants attained higher yield in the year when there was little reinfall during this period, which always followed the rainy season, with a relatively small amount of precipitation called "Karatsuyu"[12,23]. Duration of this relatively dry midsummer period after the rainy season usually doesn't exceed 40 days, and we usually observe around 10 mm of rainfall for every 5 days even during this period in Japan (Fig. 1). Therefore, soil moisture depletion should be far small even in the midsummer compared with the arid and the semi-arid regions. Crop plants could withstand soil moisture depletion by developing an elongated root system under the conditions where soil moisture decreases gradually. However, after they grow under sufficient soil moisture conditions, they could not adapt to the significant and rapid soil water fluctuations due to shallow and poorly developed root systems and, therefore, would suffer from water deficits even when soil moisture doesn't deplete considerably. Summer field crop plants in many regions of Japan would develop vigorously during the vegetative phase in the rainy season, when there is much precipitation and a low atmospheric vapor pressure deficit, from early June to mid July (Fig. 1 and 2). They would develop large shoots with shallow and poorly developed root systems. As a result, they would suffer from water deficits in the hot and relatively dry summer even if soil moisture depletes only at the surface layers of the soil.

In order to confirm this assumption, we investigated the differences in growth patterns and ecophysiological characteristics of soybean plants grown under sufficient and deficient soil moisture conditons before flowering. Then it was inquired the effects of the growth patterns and characteristics acquired by the plants before flowering on dry matter production during ripening and yield under the deficient soil moisture conditions.

Experiments were undertaken in 1984 and 1989 with relatively dry summers. As the same results were obtained in both years, we will

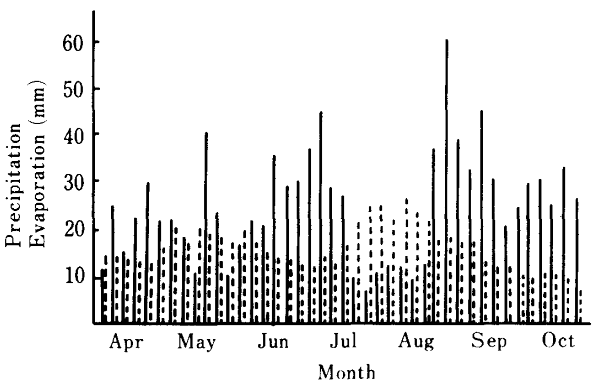

Fig. 1. Precipitation (solid lines) and evaporation (dotted lines) of every 5 days from April to October in Tokyo*.
*Average of 10 years from 1967 to 1976.

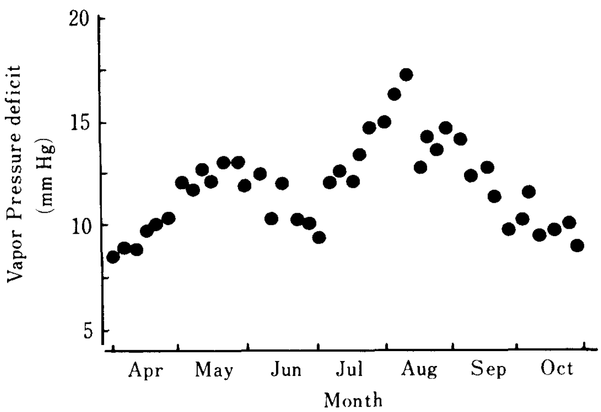

Fig. 2. Daily maximum atmospheric vapor pressure deficit* from April to October in Tokyo.
*Calculated from daily maximum temperature and daily minimum humidity. Every point represents the average of 5 days. Average of 10 years from 1974 to 1983.

describe the experiment of 1989 in this report.

Materials and Methods

Soybean plants (*Glycine max* (L.) Merr., cv. Enrei) were grown in the University farm on the Tama river alluvial soil at a planting density of 16.7 per m^2. Fertilizers were applied as basal dressing at the rates of 30, 100, 100 kg per ha for N, P_2O_5, K_2O, respectively. After irrigation was done at a depth of 10 mm at planting in order to stimulate uniform germination, some plants were grown under deficient soil moisture by withholding irrigation water (D-plot) and others were grown under sufficient soil moisture by irrigation two or three times in a week (W-plot) during the vegetative stage. At the flowering stage, plants of the D-plot were irrigated sufficiently until soil moisture of the plot was attained similar to that of the W-plot. Thereafter plants of both plots were given no water until harvesting time. Each plot was 36 m^2 (4.8 by 7.5 m). The field was isolated from rain water by covering with a tent, which was originally designed for preventing cracking of cherry fruits due to rain.

Soil moisture tension at high soil water potentials (higher than -0.1 MPa) was measured with tensiometers. At low soil water potentials, soil electric resistance was measured with gypsum blocks and soil water potential was determined using the resistance vs. soil matric potential relationship. Soil water content was measured on a dry weight basis by drying soil at 105°C in an oven, and volumetric soil water content was calculated by multiplying the soil water content on a dry weight basis by the bulk density of the soil at each soil layer. The increase of soil moisture due to rain, which accompanied the typhoon and the thunderstorm, was estimated from the difference in soil moisture immediately before and after the rain at each soil layer. Moderate fifteen to twenty plants were selected in each plot for measuring the shoot dry weight and leaf area. They were dried at 90°C in a ventilated oven and weighed.

Root length density at various depth of soil layers was measured by a core sampling method[4] using a steel sampling tube of 32 mm inner diameter. Root length at various depth of soil was also measured with the minirhizotron root observation tube system[4,5], where transparent tubes of 60 mm outer diameter and of 1.6 m length were equipped into the soil with the installation angle of 30° from the vertical. Roots on the surface of the tube were observed using a fiber-optic system (Model 1F11D4 ; Olympus Inc.) and recorded with a color video camera (Victor Inc.)[9]. The length of roots collected with the sampling tube and length of roots on the surface of the observation tube were measured by the line intersect method[25].

Leaf xylem water potential was measured with a pressure chamber (Model 3005 ; Soil Moisture Equipment Inc.) on a terminal leaflet of trifoliate leaves. The leaflet was covered with a moist polyethylene bag immediately before excising. The cylindrical inner wall of the pressure chamber was covered with wet filter paper. The chamber was pressurized with compressed nitrogen at a rate of about 0.003 MPa s^{-1}.

Photosynthetic rate and transpiration rate for calculating leaf diffusive conductance were measured with an acrylic assimilation chamber (30 mm×40 mm×5 mm) clamped over the central portion of an attached terminal leaflet. The air of which CO_2 concentration and dew point were controlled to about 350 μl l^{-1}, and about 15°C, respectively, was pumped into the chamber located on the upper and the lower side of the leaflet at a rate of 1.5 l min^{-1} adjusted with a mass flow controller (Model SEC-521 ; STEC Inc.). The change in CO_2 concentration and dew point of the air pumped into the chamber during measurements was less than 0.1 μl l^{-1} and 0.1°C, respectively. The difference in CO_2 concentration between the air pumped into and away from the chamber was measured with an infrared CO_2 analyzer (Model ZAP ; Fuji Electric Inc.). Dew point of the air pumped into and away from the assimilation chamber was measured with a dew point meter (Model 660 ; EG & G Inc.). Leaf temperature was measured with a copper-constantan thermocouple of 0.1 mm diameter attached on the lower leaf surface and did not exceed 35°C even during midday measurements except the leaves with low stomatal conductance. Leaf diffusive conductance was calculated from transpiration rate, leaf temperature and air humidity in the chamber according to Gaastra[6]. Measurements were taken under sunlight

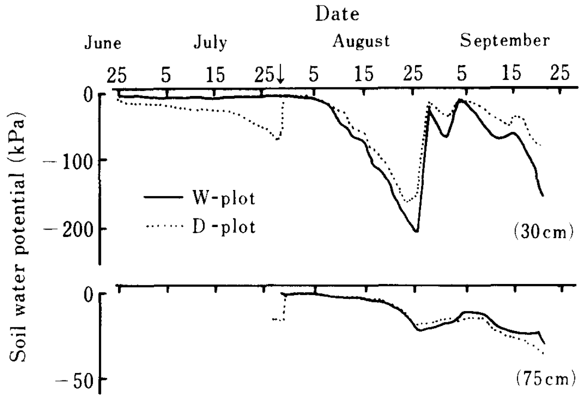

Fig. 3. Changes in soil water potential at the depth of 30 cm and 75 cm from the soil surface. Arrow indicates the date when flowering started. Soil moisture increase on August 28 and September 3 was due to rain, which accompanied a typhoon and a thunderstorm.

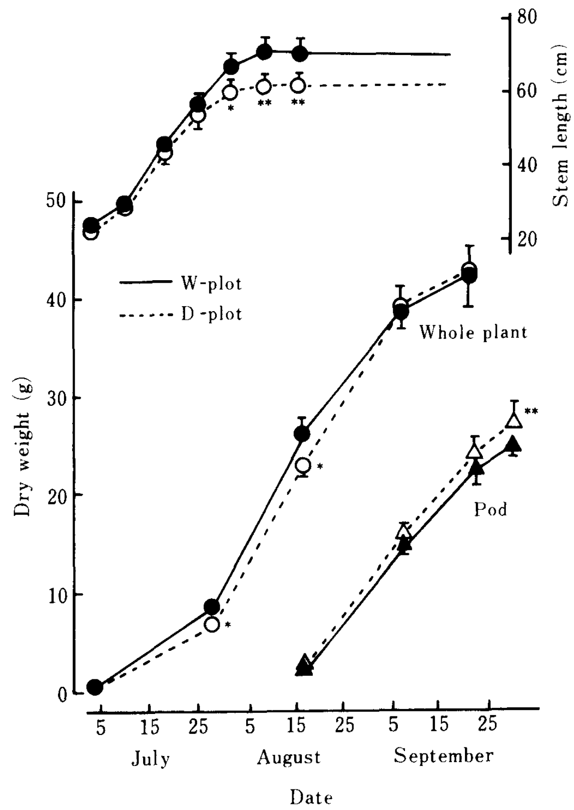

Fig. 4. Changes in stem length and dry weight of the whole plant and pod per plant. Virtical bars represent standard deviations. One asterisk (*) and two asterisks (**) represent that means are significantly different at 5% and 1%, respectively.

more than 1,200 μE m^{-2}s^{-1} or under artificial light (Model LA-100; Hayashi-Tokei Inc.) of 1,600 μE m^{-2}s^{-1} on leaf surface.

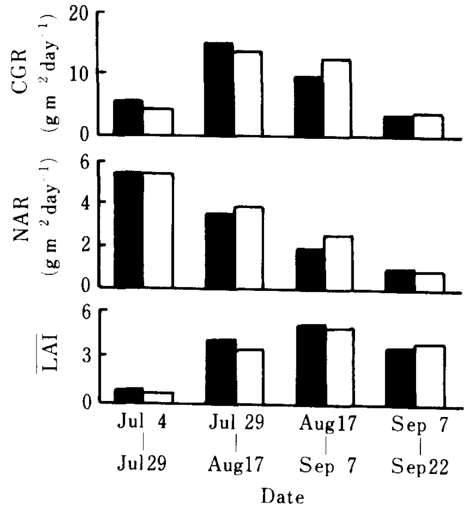

Fig. 5. Changes in crop growth rate (CGR), net assimilation rate (NAR) and mean leaf area index ($\overline{LAI}$) in the plants of the W-(solid bars) and of the D-(open bars) plots.

Transpiration rate of a whole leaflet was measured on an attached terminal leaflet with the acrylic assimilation chamber designed by Tsunoda[12,26]. The air of controlled dew point was pumped into the chamber at the rate of 8.0 l min^{-1}.

Results

1. Differences in growth and morphological characters between the plants under sufficient (W-plot) and deficient (D-plot) soil moisture conditions before flowering

Soil water potential at a depth of 30 cm was around −6.9 KPa during the vegetative stage in the W-plot. It decreased gradually down to −67.6 KPa at flowering time in the D-plot (Fig. 3). Main stem length, which was determined almost until flowering time, and dry weight of the above ground part were significantly smaller in the plants of the D-plot than those of the W-plot before flowering (Fig. 4). Leaf area per plant on July 29 was 1,769 cm^2 and 1,410 cm^2 in the W- and D- plot, respectively. Low leaf area index (LAI) was responsible for the low crop growth rate (CGR) in the plants of the D-plot (Fig. 5) and, therefore, they produced low dry matter (7.1 g per plant) compared with those of the W-plot (8.7 g) on July 29. On the other hand, the root length density, measured by the core sampling method, and root length, measured with the minirhizotron root observation tube system,

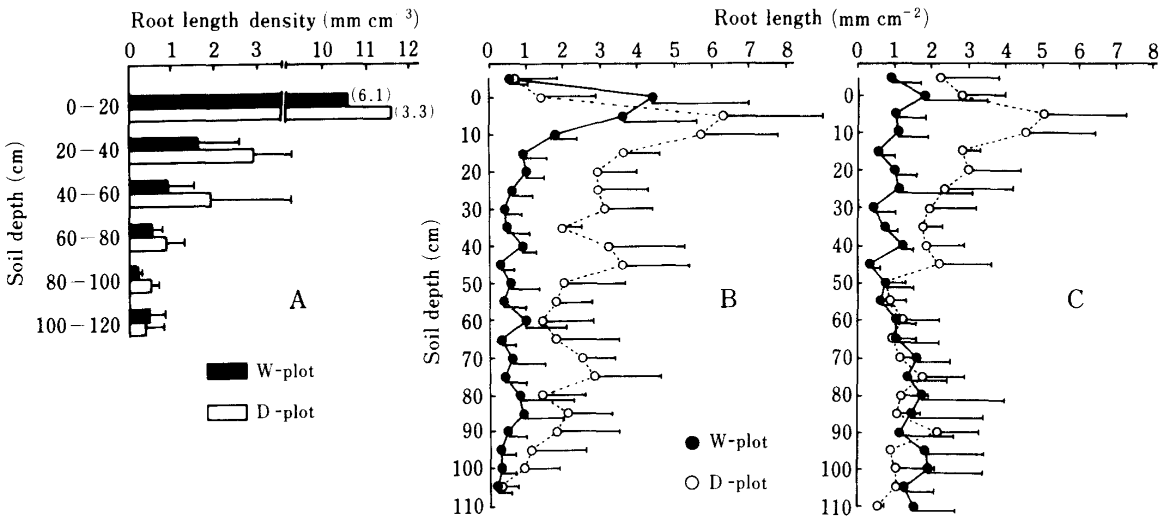

Fig. 6. Comparisons of vertical root distribution between the plants of the W- and the D-plots. A : Root length density measured by the core samplng method on July 26. B, C : Root length measured with the minirhizotron root observation tube system on July 27 (B) and September 20(C). Figures in the parentheses and horizontal bars represent standard deviations of five replications.

from surface soil layers to deep soil layers were large in the plants of the D-plot compared with those of the W-plot at flowering time (Fig. 6A and B). It was clear from these results that the growth of above ground part was suppressed, but that root systems developed well in the plants of the D-plot compared with those of the W-plot.

2. Differences in growth and eco-physiological characteristics between plants in the W- and D- plots with decreasing soil moisture after flowering

Irrigation continued in the D-plot until the soil moisture became similar to that in the W-plot and thereafter it was withheld from plants in both plots. Soil moisture depleted significantly in both plots until August 26 (Fig. 3). Soil moisture increased remarkably due to heavy rain, which accompanied a typhoon on August 28 and a thunderstorm on September 3, and, thereafter, decreased again. There became no differences in root length at the deep soil layers between the two plots at the ripening stage because of a significant increase in the root length of the plants of the W-plot although root length at the shallow soil layers was still larger in the plants of the D-plot than among those in the W-plot (Fig. 6C). No differences in dry weight were seen between the plants of both plots on September 7 and 22 (Fig. 4) due to the large CGR of the period from August 17 to September 7 in the plants of the D-plot compared with those of the W-plot (Fig. 5). High NAR was responsible for the significant increase of CGR in the plants of the D-plot (Fig. 5). The difference in pod weight increased gradually after September 7 and the significant difference was observed at the end of September (Fig. 4). As shown in Table 1, seed yield was larger by about 0.5 Mg/ha in the plants of the D-plot than those of the W-plot due to a larger number of fully ripened seeds. And this might also be due to higher weight of a seed in the plants of the D-plot although there was no significant difference in the mean of the weight. Stem weight and seed-stem ratio at harvest time seemed slightly higher in the plants of the D-plot than in the W-plot although there was no significant difference (Table 1). Higher seed yield in the D-plot might result from higher dry matter production during the ripening stage and also higher harvest index.

These results indicated that the plants of the D-plot developed root systems well and kept NAR high under deficient soil moisture conditions, leading to high dry matter production and also high yield compared with the plants of the W-plot. Therefore, we investigated in turn how the D-plot kept higher NAR.

The amount of soil moisture depletion in relatively deep soil layers at a depth of 40 cm

Table 1. Yield and yield components in the plants of the W- and the D-plots.

Plots	Seed no. per plant	100 seed wt.* (g)	Seed wt. per plant* A (g)	Unit area sampling yield* (Mg ha^{-1})	Stem wt. per plant B (g)	A/B (g g^{-1})
W	58.4a**	26.3a	15.4a	3.07a	6.6a	2.3a
D	67.0b	27.3a	18.3b	3.55b	7.7a	2.4a

* Weight at 15% moisture.

** Means followed by the different letters are significantly different at 5% level.

Table 2. Depletion of soil moisture at various soil depth during July 31 to September 11 (A) and during September 11 to September 26 (B)*.

Soil depth	Field capacity		Depletion of soil moisture (mm)			
			A		B	
(cm)	(g cm^{-3})	(mm)	W-plot	D-plot	W-plot	D-plot
0— 20	51.9	103.5	42.5	44.5	12.5	19.5
20— 40	53.3	107.0	29.0	30.0	15.5	21.0
40— 60	58.0	116.0	48.0	56.0	10.5	11.5
60— 80	54.9	109.5	35.5	52.5	13.0	−2.0
80—100	55.6	111.0	25.0	21.0	0.5	5.5
Total	—	547.0	180.0	204.0	52.0	55.5

* The increase of soil moisture due to rain water, which accompanied the typhoon and the thunderstorm, was estimated from the difference in soil moisture immediately before and after the rain at each soil layer.

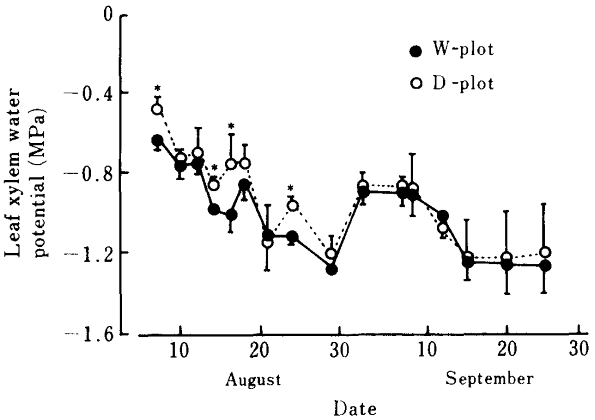

Fig. 7. Changes in leaf xylem water potential** during daytime after withholding water from the plants of the W- and the D-plots. Vertical bars represent standard deviations of three replications.

*Means are significantly different at 5% level.

**The third leaf from the uppermost was used for measurements.

from the surface to a depth of 80 cm was high in the D-plot for 43 days from July 31 to September 11, even though there were no clear differences in soil moisture depletion of the relatively shallow soil layers to the depth of 40 cm from the surface (Table 2). The total amount of depleted water from the surface to the depth of 100 cm was considerable high in the D-plot compared with the W-plot. During the late ripening stage from September 11 to September 26, no differences in the total amount of water depletion were observed between the two plots.

After withholding water, leaf xylem water potential during the daytime decreased in the plants of both plots until August 29 (Fig. 7). Leaf xylem water potential became significantly higher at the beginning of September due to the increase in soil moisture content and decreased again thereafter. During the flowering to the early ripening stages, from August 7 to 29, leaf xylem water potential tended to be higher in the plants of the D-plot than those of the W-plot. However, during the late ripening stage after September 7, significant differences in the potential were not observed. Transpiration rate-leaf xylem water potential ratio under intense transpiration, which represents the water uptake capability of plants grown under deficient soil moisture[15], was significantly larger in the plants of the D-plot than those of the W-plot at the early ripening stage (Table 3). It is well known that photosynthetic rate of soybean plants[7,12], as well as rice plants[11], reaches the maximum in the morning and then decrease due to water stress even under sufficient soil moisture conditions in the late morning and in the afternoon. And the degree of the depression increase with the reduction of soil moisture[12,24]. We compared the midday depression of the photosynthetic rate in the afternoon under sufficient solar radiation for photosynthesis. The degree of the depression in photosynthetic rate (Table 4) was significantly lower in the plants of the D-plot on August 21 at the early ripening stage. The midday depression of leaf diffusive conductance was also small in the plants of the D-plot compared with the W-plot (data are not shown).

Table 3. Comparison in transpiration rate (T)- leaf xylem water potential(Ψ_x) ratio (T/Ψ_x)* between the plants in the W-and the D-plots at the early ripening stage (August 22).

Plots	T/Ψ_x ($gH_2O\ dm^{-2}\ h^{-1}\ MPa^{-1}$)
W	4.5 (0.2)a**
D	5.0 (0.4)b

* Ratio at −0.91 to −1.23 MPa xylem water potential of the fully expanded upper leaves.

** Figures in the parentheses represent standard deviations of seven (W) and six (D) replications. Means followed by the different letters are significantly different at 5% level.

However, differences in the degree of the midday depression of the photosynthetic rate were not observed between the two plots on September 20 at the late ripening stage.

The differences in photosynthetic rate between plants of the two plots, measured under artificial light in the early morning, were observed at the flowering and early ripening stages (Fig. 8). Photosynthetic rates of leaves attaching to lower positions on a stem were slightly higher in the plants of the D-plot than those in the W-plot on August 5, when upper leaves on a stem were expanding and their photosynthetic rates were small compared with those of expanded young leaves. On September 6, when all leaves had fully expanded, and the photosynthetic rate began to decrease even in upper leaves due to senescence, the photosynthetic rate was higher in the plants of the D-plot than in those of the W-plot. Especially larger differences were observed in the leaves attached to lower positions. However, at the late ripening stage, there were no clear differences in the photosynthetic rate between the plants of the two plots.

Discussion

It is well known that, in plants grown under deficient soil moisture, roots continue to elongate. The growth of the above ground part such as stem elongation and leaf expansion was suppressed and, therefore, the root-shoot ratio is large compared with plants grown under sufficient soil moisture[16,19,21,27]. It was also observed that in soybean plants of the D-plot grown under deficient soil moisture before flowering, stem length, leaf area and dry weight of the above ground part were

Table 4. Comparisons of the maximum rate in the morning and the minimum rate in the afternoon under sufficient light intensity above 1,400 $\mu mol\ m^{-2}s^{-1}$ during diurnal change of photosynthetic rate*.

Date	Plots	Maximum rate (A) ($mgCO_2dm^{-2}h^{-1}$)	Minimum rate (B) ($mgCO_2dm^{-2}h^{-1}$)	Declining percentage (1-B/A)×100
Aug.21	W	49.0 (1.0)**	34.6 (4.2)	29.5 (7.9)a***
	D	43.7 (2.4)	35.9 (2.8)	17.8 (4.5)b
Sep.20	W	18.9 (3.5)	10.3 (2.3)	43.6 (14.8)a
	D	17.6 (6.0)	8.8 (4.9)	48.3 (19.8)a

* Five to seven fully expanded upper leaves were used for measurements.

** Figures in the parentheses represent standard deviations.

*** Means followed by the different letters are significantly different at 5% level.

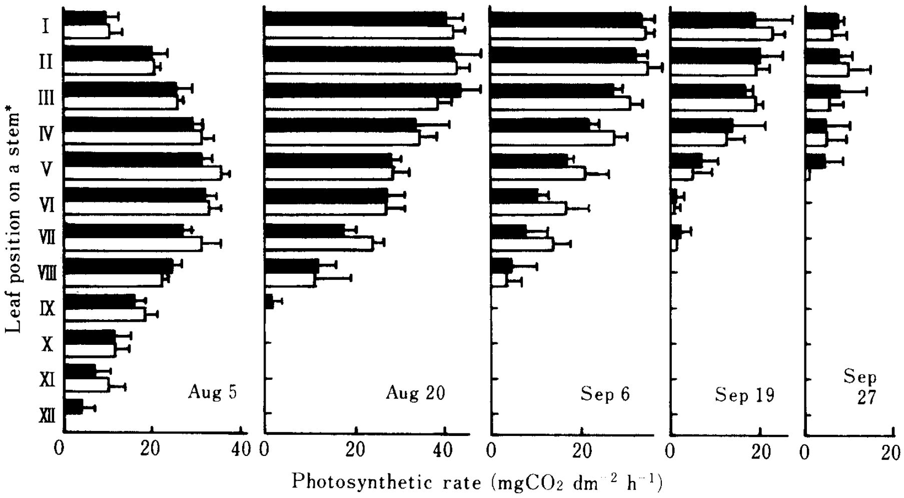

Fig. 8. Photosynthetic rate of leaves at different positions on a stem in the morning under sufficient artificial light of above 1,600 μmol $m^{-2}s^{-1}$. Solid and open bars represent the plants of the W- and the D-plot, respectively. Bars represent standard deviations of five replications except Sept. 19 (three replications).

*I, II, ---- XII indicate the position of the leaf counted from the uppermost leaf on a stem.

small (Fig. 4) and root length was large in both shallow and deep soil layers (Fig. 6) compared with those of the W-plot grown under sufficient soil moisture. Under deficient soil moisture achieved by withholding water from both plots after flowering, CGR during the flowering to early ripening stages was large in the plants of the D-plot due to the large NAR (Fig. 5) and as a result, yield was high compared with plants of the W-plot (Table 1). Under deficient soil moisture conditions during the flowering to early ripening stages, the capacity for absorbing soil water indicated by transpiration-leaf water potential ratio was high (Table 3). In resistance to water flow from soil through plants, soil resistance-root resistance ratio decreased with the increase in root density[17]. And water uptake per unit root length was larger in roots at deeper soil layers than in roots at shallower soil layers under the deficient soil moisture conditions[28]. The difference in the capacity for absorbing soil water between the W- and the D-plot might be due to the difference in root system development. Indeed, amount of water uptake from relatively deep soil layers was high in the plants of the D-plot compared with those of the W-plot (Table 2). As a result, leaf xylem water potential during daytime was kept high (Fig. 7) in the plants of the D-plot compared with those of the W-plot while leaf xylem water potential decreased from -0.5 and -0.7 MPa to -1.2 MPa. Because the small reduction in leaf water potential in the range from -0.6[10] to -1.5 MPa[2] reduced photosynthetic rate remarkably in soybean plants, the degree of the midday reduction in photosynthetic rate was smaller in the D-plot under deficient soil moisture conditions (Table 4). And even under sufficient soil moisture conditions immediately after irrigation, the degree of the midday depression should be less in the D-plot as observed before[7]. Therefore, the plants of the D-plot did not suffer from water stress with the reduction in soil moisture compared with the W-plot. Moreover, the decrease in photosynthetic rate due to leaf senescence was delayed in the plants of the D-plot (Fig. 8) where the root system was developed well and midday leaf xylem water potential was kept high. High NAR during the flowering and the early ripening stages in the plants of the D-plot compared with those of the W-plot was concluded to result from (1) the well-developed root system of the D-plot plants in the deep soil dayers, (2) high absorption of water in deep soil layers where soil moisture was kept high even though soil moisture in shallow soil layers was depleted[1,3,19,28], (3) maintenance of high leaf water potential in the daytime[1,3] and of high photosynthetic rate during daytime[12,24] and (4) the delay in the decrease in photosynthetic rate due to senescence.

It was interesting enough that plants with a well-developed root system could delay not only water deficits but also leaf senescence. Water stress promotes leaf senescence[18]. It had also been observed in rice plants that the plants with well-developed root systems indicate high root physiological activity[14,22] and send a large amount of cytokinins from root to shoot[22]. As a result, they could delay leaf senescence during the ripening stage[14,22]. The difference in water stress and root system development, which may be related to the root physiological activity, might induce the differene in leaf senescence between the plants of the D- and W-plots.

At the late ripening stage, there were no differences in the root length of the deep soil layers between the plants of both plots due to the increase in the W-plot and the decrease in the D-plot although the differences in root length of shallow soil layers still existed (Fig. 6). There were no differences in daytime leaf xylem water potential (Fig. 7), the degree of the midday depression in photosynthetic rate (Table 4) and the reduction in the photosynthetic rate due to senescence (Fig. 8).

The plants in the W-plot might transpired much water because of large leaf area. However, they could not absorb enough water due to poor developed root system. Because they could not develop root system immediately they suffered severe water stress for a while after withholding irrigation compared with the plants in the D-plot. About one month after withholding irrigation, root density in deeper soil layers increased in the plant in the W-plot (Fig. 6) and there were no clear difference in water deficits between the W- and the D-plots (Fig. 7). Development of root system would be important for keeping water uptake capacity high and, therefore, attaining high photosynthesis and dry matter production under deficient soil moisture conditions[19].

As this experiment was conducted in the loamy soil where field capacity and readily available water are high (Table 2)[15], reduction of soil moisture was not large even though irrigation was withheld from the plants after flowering. Soil water potential did not decrease less than - 200 KPa, even at the 30 cm of the soil depth, and less than - 30 KPa at 75 cm of soil depth (Fig. 3). Under such small reductions of soil moisture, the significant difference in net assimilation rate and dry matter production during ripening under deficient soil moisture was observed (Fig. 4 and 5). The effect of root system development on growth and dry matter production under deficient soil moisture conditions will be more remarkable in the soil with the small amount of readily available water. In the sandy soil, where field capacity and readily available water are very low, extreme differences in growth were observed ; that is, soybean plants, which had developed a shallow root system under sufficient soil moisture conditions, suffered severe water stress and shed many leaves only 3 weeks after withholding irrigation from the plants, compared with plants which had developed a deeper root system under deficient soil moisture conditions[8].

Conclusion

In this research we could confirm the assumption that summer field crop plants in Japan would develop large shoots but poor root systems during the rainy season called "Baiu" and this would enlarge the adverse effects of soil moisture depletion on dry matter production under the deficient soil moisture condition in summer thereafter. It was concluded that soil moisture control through improved cultivation practice, such as drainage in the rainy season, for a well developed elongated root system should be effective in reducing the adverse effects of soil moisture fluctuation on crop plants, although irrigation in the dry midsummer was done to reduce it. It has also been pointed out that development of root system would be important for keeping the leaf photosynthetic rate high and attaining high dry matter production even under sufficient soil moisture conditions[7]. Improved cultivation or breeding for a well developed root system would be very important in Japan where summer field crop plants are grown under the humid conditions of sufficient soil moisture and low evaporation in the first half of their growing season.

References

1. Angus, J.F., S. Hasegawa, T.C. Hsiao, S.P. Liboon and H.G. Zandstra 1983. The water balance of

post-monsoonal dryland crops. J. Agric. Sci. 101 : 699—710.

2. Boyer, J.S. 1970. Differing sensitivity of photosynthesis to low water potentials in corn and soybean. Plant Physiol. 46 : 236—239.
3. ————, R.R. Johnson and S.G. Saupe 1980. Afternoon water deficits and grain yields in old and new soybean cultivars. Agron. J. 72 : 981—986.
4. Böhm, W. 1979. Methods of Studying Root Systems. Springer-Verlag, Berlin. 1—188.
5. Brown, D.A. and D.R. Upchurch 1987. Minirhizotrons : A summary of methods and instruments in current use. In Taylor, H.M. ed., Minirhizotron Observation Tubes : Methods and Applications for Measuring Rhizosphere Dynamics. Am. Soc. Agron., Crop Sci. Soc. Am. Soil Sci. Soc. Am., Madison. 1—13.
6. Gaastra, P. 1959. Photosynthesis of crop plants as influenced by light, cabon dioxide, temperature and stomatal diffusive resistance. Mededel. Landbouwhogesh. Wageningen 59 : 1—68.
7. Hirasawa, T., M. Nakahara and K. Ishihara 1988. Comparisons of growth and physiological and ecological characteristics between soybean plants grown under different soil moisture conditions. Jpn. J. Crop Sci. 57 (Extra 2) : 155—156**.
8. ———— and K. Inada 1991. Varietal and interspecific differences of water uptake capacity under deficient soil moisture in crop plants. In Reports of Joint Research in 1991. Tottori Univ. Arid Land Res. Cen., Tottori. 3—4**.
9. ————, M. Takei and K. Ishihara 1995. A minirhizotron method for measuring root system of soybean plants growing in the field. Jpn. J. Crop Sci. 64 (in press).
10. Ishihara, K., T. Takai and T. Hirasawa 1984. Effects of air humidity and leaf water potential on photosynthetic rate of soybean plants. Jpn. J. Crop Sci. 53 (Extra 1) : 76—77**.
11. ———— and K. Saito 1987. Duirnal course of photosynthesis, transpiration, and diffusive conductance in the single-leaf of the rice plants grown in the paddy field under submerged condition. Jpn. J. Crop Sci. 56 : 8—17*.
12. Huck, M.G., K. Ishihara, C.M. Peterson and T. Ushijima 1983. Soybean adaptation to water stress at selected stages of growth. Plant Physiol. 73 : 422—427.
13. Ishida, Y. 1992. Influence of environmetal factors in baiu season to the growth, development and yield of groundnut (*Arachis hypogaea*) in Japan (1). J. Saitama Univ. (Fac. Educ.). 42 : 23—31**.
14. Jiang, C.Z., T. Hirasawa and K. Ishihara 1988. Physiological and ecological characteristics of high yielding varieties in rice plants. II. Leaf photosynthetic rates. Jpn. J. Crop Sci. 57 : 139—145*.
15. Kramer, P.J., 1983. Water Relations of Plants. Academic Press, New York. 1—489.
16. Meyer, R.F. and J.S. Boyer 1981. Osmoregulation, solute distribution, and growth in soybean seedling having low water potentials. Planta 151 : 482—489.
17. Newman, E.I. 1969. Resistance to water flow in soil and plant. I. Soil resistance in relation to amounts of roots : Theoretical estimates. J. Appl. Ecol. 6 : 1—12.
18. Nooden, L.D. 1988. The phenomena of senescence and aging. In Nooden, L.D. and A.C. Leopold, eds., Senescence and Aging in Plants. Academic Press, San Diego. 1—50.
19. Proffitt, A.P.B., P.B. Berliner and D.M. Oosterhuis 1985. A comparative study of root distribution and water extraction efficiency by wheat grown under high- and low frequency irrigation. Agron. J. 77 : 655—662.
20. Research Society of Farmland Agriculture 1988. Basis of Farmland in Japan. Its Present Situation and Trends. Agricultural Upland Development Association, Tokyo. 1—493**.
21. Sharp, R.E., W.K. Silk and T.C Hsiao 1988. Growth of the maize primary root at low water potentials I. Spatial distribution of expansive growth. Plant Physiol. 87 : 50—57.
22. Soejima, H., T. Sugiyama and K. Ishihara 1992. Changes in cytokinin activities and mass spectrometric analysis of cytokinins in root exudates of rice plant (*Oryza sativa* L.). Plant Physiol. 100 : 1724—1729.
23. Takahashi, Y. 1976. Cultivation and growth of groundnut. In Soybean, azuki bean and groundnut. Nobunkyo, Tokyo. 89—118**.
24. Tazaki, T., K. Ishihara and T. Ushijima 1980. Influence of water stress on the photosynthesis and productivity of plants in humid area. In Turner, N.C. and P.J. Kramer, eds., Adaptation of Plants to Water and High Temperature Stress. John Wiley & Sons, New York. 309—321.
25. Tennant, D. 1975. A test of a modified line intersect method of estimating root length. J. Ecol. 63 : 995—1001.
26. Tsunoda, S. 1974. Methods for measuring photosynthesis. In Matsuo, T. ed., Handbook of Plant Breeding. Yokendo, Tokyo. 170—174**.
27. Westgate, M.E. and J.S. Boyer 1985. Osmotic adjustment and the inhibition of leaf, root, stem and silk growth at low water potentials in maize. Planta 164 : 540—549.
28. Yoshida, S. and S Hasegawa 1982. The rice root system : Its development and function, In Drought Resistance in Crops with Emphasis on Rice. IRRI, Los Banos. 97—114.

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