水不足に対するダイズの馴化(3):

誌名	日本作物學會紀事
ISSN	00111848
著者	伊藤, 亮一 玖村, 敦彦
巻/号	56巻1号
掲載ページ	p. 109-114
発行年月	1987年3月

Japan. Jour. Crop Sci. 56(1) : 109—114 (1987)

Acclimation of Soybean Plants to Water Deficit

III. Changes in leaf growth as regulated by "leaf extensibility" and pressure potential under various soil water regimes*

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Received July 31 1986

In our previous paper[6], it was shown that the increasing rate of the total leaf area of a single soybean plant was strongly depressed immediately after reducing soil water content to a low level, and that it recovered to a fairly large extent thereafter even though the soil water content was maintained at the same low level. This result suggests that a kind of acclimation occurs during leaf growth of soybean plants when water stress is prolonged. The objectives of this paper are to confirm the phenomenon, and further, to find out the physiological basis for it at the level of a single leaf.

Since the turgor pressure of the leaf tissue cells is undoubtedly the motive force of leaf expansion[1,11], it is thought to be one of the internal factors regulating the rate of leaf expansion.

In addition to this, the degree of extension of the leaf tissues by a given stress, that is, their physical extensibility is also thought to be another factor regulating the leaf expansion rate[4,8].

Thus, we investigated the physiological basis of acclimation in leaf growth to soil water regimes from the view points of (1) pressure potential of leaf tissues and (2) "leaf extensibility" measured by the procedure described later.

Materials and Methods

Materials and their growing condition

Seeds of soybean plant (cv. Norin No.2) were sown in 3 liter plastic pots filled with soil on October 5, 1985. The plants were grown in a controlled room (natural light with supplemental artificial illumination to lengthen day period ; day/night period, 15/9 hr ; day/night temperature, 27/22°C ; relative humidity, ca. 70%).

When the 8th leaves were expanding, the pots were grouped into two (this day is called "day 0" and days in the treatment period will be called according to the days after day 0) and thereafter, in one group soil water content (SWC, expressed as the percentage of field capacity and on the daily average) was maintained at 80% level (Treatment H). In the other group, after day 0, watering was withheld for a while and on day 3, when SWC decreased to 45%, it was resumed and thereafter, SWC was maintained at 45% level during the treatment period (Treatment L).

On days 3 and 15, a part of pots of Treatment L were watered sufficiently (Treatments $(L\text{-}H)_1$ and $(L\text{-}H)_2$, respectively).

Procedures for measurements

Leaf growth: The length of the central leaflets of the 8th trifoliolate leaves was measured with a ruller every day at 4 p.m.

Water potential (Ψ), *osmotic potential* (π) *and pressure potential* (P) *of leaves*: The Ψ was measured by the compensation method[10]. The leaf strips (1×9mm) were floated on mannitol solution of different concentrations for 4 hours. The changes in length of the leaf strips in the period were measured with a dissecting microscope. The Ψ value of the leaf was calculated from the relation between changes in the strip length and the water potential of mannitol solution as shown in Fig. 1.

The π was measured with an osmometer (Wescor 6100B).

The P was calculated as the difference

* Experiments for this study were conducted in the Center of Environment Regulation System for Biology, The University of Tokyo. A part of this work was presented at the 181st meeting of the Crop Science Society of Japan, April 7, 1986.

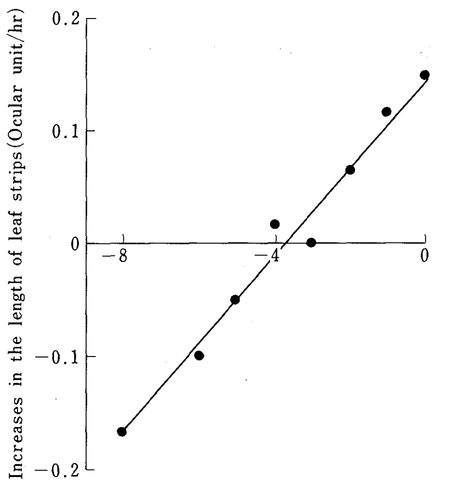

Fig. 1. Changes in the length of leaf strips floating on the mannitol solution of various water potentials. The leaf water potential was estimated with the interception of abscissa. A dot in the figure is the mean of five measurements.

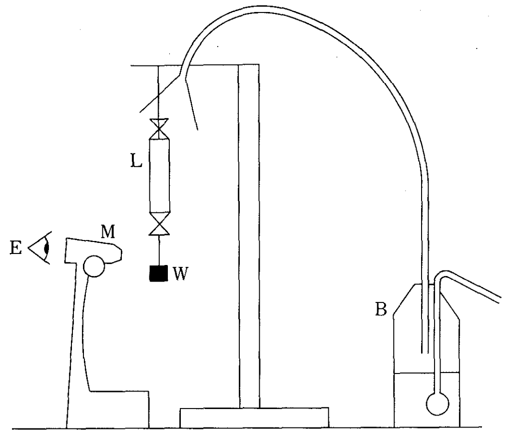

Fig. 2. The outlines of an apparatus for the measurement of leaf extensibility. The leaf strip (L) was attached to weight (W). The changes in leaf length were measured with a disecting microscope (M). The air humidified through water in a bottle (B) was sent to the surroundings of leaf strips. E denotes human eyes.

between Ψ and π.

Leaf extensibility: As shown in Fig.2, a weight (9.0g) was attached to the tail end of a leaf strip (8×30 mm). The atmospheric temperature was regulated at ca. 25°C and vapor saturated air at the temperature was sent to the surroundings of the leaf strips. The changes in the leaf strip length with time after attaching the weight was observed with a dissecting microscope.

Fig.3 is an exsample of time courses of the strip length. In general, the length increased rapidly in the first one minute probably due to stretching of wrinkles of the tissues. After that, it increased at a nearly constant rate for a while. Thus, the rates of extension of the leaf strips in the period between 1 and 5 minutes were calculated and named "leaf extensibility" (Ex). We think Ex obtained according to the above mentioned procedure can be used as an index of physical extensibility of leaf tissues.

Results

Leaf growth

Figs.4 and 5 show the leaf length and the rate of leaf growth, respectively. In Treatment H, the leaf extended rapidly and reached the final size at the middle of the treatment period. In Treatment L, after the start of the treatment, the leaf growth slowed down and then completely stopped growing for two days. After that, however, it was resumed though there was no change in SWC. The leaf growth rate after the resumption was lower than that of Treatment H in the rapid growth period. The leaf of Treatment L continued its growth for a while and attained its final size much later than that of Treatment H. The final leaf size of Treatment L was definitely smaller than that of Treatment H.

In Treatments $(L\text{-}H)_1$ and $(L\text{-}H)_2$, leaf growth was accelerated by sufficient water supply. Yet the leaf growth rates after water supply in these treatments were still lower than that in Treatment H.

Ψ, π and P

Fig.6 shows the time courses of Ψ and π in the treatment period. In Treatment H, the leaf maintained a high and constant Ψ level during the treatment period. The level of π was also high and nearly constant.

In Treatment L, Ψ decreased after withholding water and after day 3, mantained a low and nearly constant level. In this treatment, π continued decreasing until day 6 though Ψ was kept constant between day 3 and day 6. After day 6, π seemed to increase gradually with time. In Treatments $(L\text{-}H)_1$ and (L

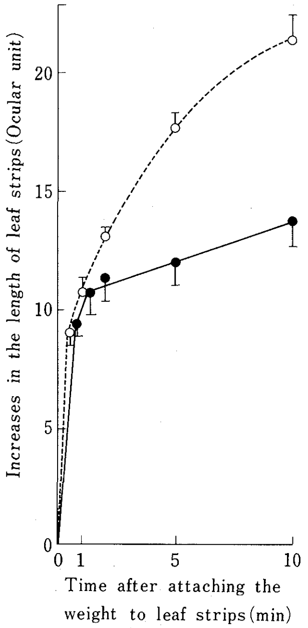

Fig. 3. The changes in leaf strip length after attached with the weight. Open and close circles denote well-watered and water stressed leaves, respectively. Each dot is the mean of four measurements and the bar indicates the range of standard error.

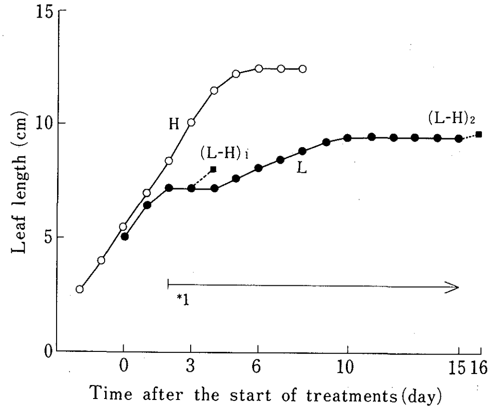

Fig. 4. Changes in leaf length after the start of treatments. The H,L, $(L\text{-}H)_1$ and $(L\text{-}H)_2$ denote the soil water treatments described in Materials and Methods. Each dot is the mean of four measurements. *1 : Soil water content in Treatment L was maintained 45% between days 2 and 15.

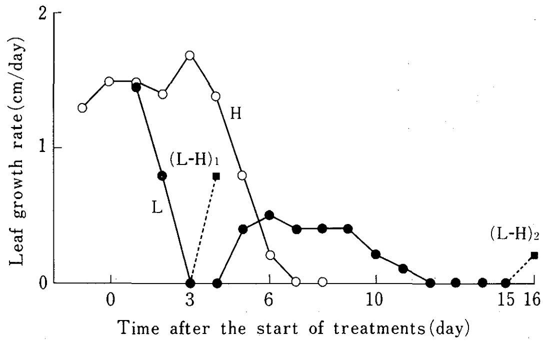

Fig. 5. Changes in leaf growth rate after the start of treatments. Each dot is the mean of four measurements.

$-H)_2$, after sufficient water supply, Ψ increased considerably but π showed little change.

Fig.7 shows the time courses of P in the treatment period. In Treatment H, P maintained a high and nearly constant level during the treatment period though the value on day 3 was a little lower than those on other days. In Treatment L, P continued decreasing until day 3. However, on that day, P turned to increase and recovered perfectly on day 6. After that there was no substantial difference in P between Treatments H and L. In Treatments $(L\text{-}H)_1$ and $(L\text{-}H)_2$, P increased rapidly after sufficient weter supply.

Leaf extensibility (Ex)

Fig.8 shows time courses of Ex in the four treatments. In Treatment H, Ex decreased as the leaf developed and after the leaf attained full expansion, it remained constant. In Treatment L, Ex decreased much more rapidly in the first two days than in Treatment H. Thereafter, in Treatment L, Ex kept decreasing gradually until day 10 and then remained constant at a level much lower than the final level in Treatment H. In Treatments $(L\text{-}H)_1$ and $(L\text{-}H)_2$, when sufficcient water was supplied after water deficit, Ex showed a small increase in the former but no change in the latter.

Relationships of leaf growth rate with P and Ex

The relationships of leaf growth with P and Ex are shown in Figs.9 and 10, respectively. Dots in parentheses in the figure were measurements after the leaves attained the final size. Leaf growth rate showed a positive correlation both with P and Ex in the growing period. The correlation was much closer with Ex than with P.

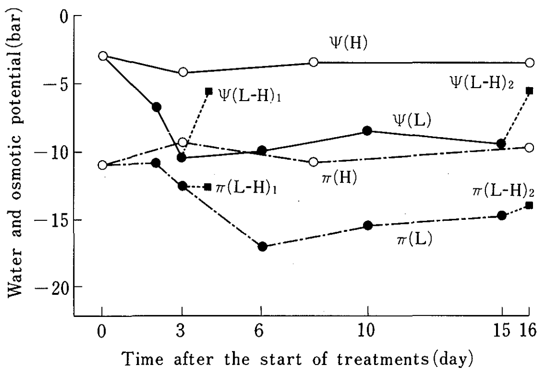

Fig. 6. Changes in water and osmotic potentials after the start of treatments. The Ψ and π denote water and osmotic potential, respectively. Each dot is the mean of five measurements.

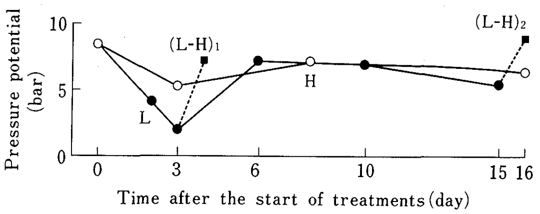

Fig. 7. Changes in pressure potential after the start of treatments. Each dot is the mean of five measurements.

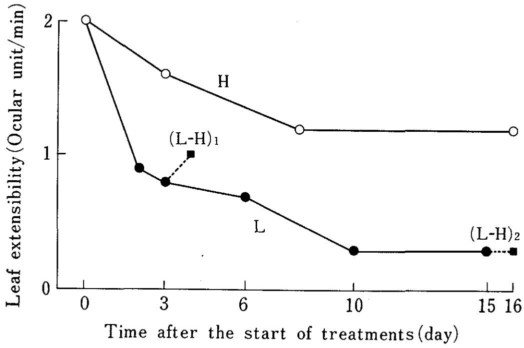

Fig. 8. Changes in leaf extensibility after the start of treatments. Each dot is the mean of four measurements.

Discussion

The leaf growth was completely inhibited by water deficit at the early time of the treatment period. However, after a while, leaves resumed growing though SWC was maintained at the same level as before (Figs.4 and 5). This clearly shows that a kind of acclimation occurs in leaf growth at the level of a single leaf when water deficit is prolonged.

The depression of leaf growth at the early stage of water deficit is attributable to the reduction in both P and Ex (Figs.7 and 8). Recovery in leaf growth after day 3 seems to be brought about by recovery in P (Fig.7).

The recovery in P after day 3 resulted mainly from a decrease in π (Fig.6). This clearly shows that the recovery of P was brought about by osmotic adjustment.

Although P recovered completely, the recovery of leaf growth was incomplete (Fig.5). The reason for this is that Ex did not recover at all and remained low until the end of the treatment period in Treatment L.

In Treatments $(L-H)_1$ and $(L-H)_2$, after sufficient water supply, very small and no change of Ex occurred, respectively. This suggests that Ex is irreversibly reduced by water stress. Such an irreversible reduction in Ex by previous water stress seems to be the reason why the recovery of leaf growth was incomplete in spite of the complete recovery in P after sufficient water supply in these treatments.

Boyer[2] observed that the leaves of sunflower plants stopped growing by water deficit treatment, but after a few days they resumed growing when the water deficit was prolonged. The leaf growth rate in the water deficit condition was lower than in the non-stressed condition. This observation of his is in accord with the result of our experiment.

It is known that the leaf growth rate is depressed by water deficit[5]. In such a case, some authors reported that there was no difference in P between stressed and unstressed plants[7,9,12], while others observed that P was depressed by water deficit[3,11]. In the former case, a factor or factors other than P have probably regulated the leaf growing process. It is pointed out that water deficit affects physical extensibility of leaf tissues[3,8].

As mentioned above, our experimental result shows that both P and "leaf extensibility" acted as regulating factors for leaf growth under various water regimes. Further analysis of processes of veriations in P and leaf extensibility becomes essential to understand physiological bases for acclimation to water deficit in soybean plants.

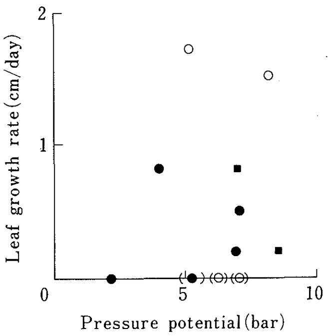

Fig. 9. The relation between pressure potential and leaf growth rate. Dots in parentheses are measurements after leaves attained the final size. The correlation coefficient is 0.16. Open and closed circles are Treatments H and L, respectively. Closed rectangles are Treatments $(L\text{-}H)_1$ and $(L\text{-}H)_2$.

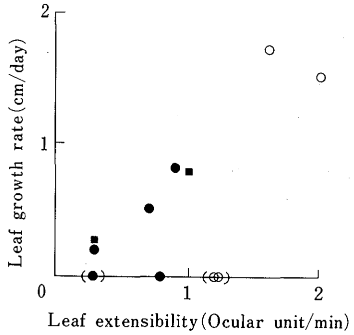

Fig. 10. The relation between leaf extensibility and leaf growth rate. Dots in parentheses are measurements after leaves attained the final size. The correlation coefficient is 0.89. The symbols used are the same as those in Fig.9.

Summary

The leaf growth of soybean plants under various water regimes was examined with special reference to leaf extensibility (Ex), i.e. the degree of extension of leaf tissues by a given stress, and pressure potential (P).

The results are summarized as follows:

1) When water supply to the plants were stopped, the leaf growth slowed down coming to a complete stop when the soil water content decreased to 45% of the field capacity. After that, however, the leaf resumed growing though there was no change in soil water content. This clearly indicates that the growth of soybean leaves acclimates to water deficit. But the leaf growth rate after the resumption was lower than that of the control.

2) When the leaf growth rate decreased by water dificit, both P and Ex decreased. After that, P of water stressed plants recovered completely due to the osmotic adjustment. The recovery of P enabled the leaf to grow again. On the contrary, Ex remained low and did not recover. This was considered to be the reason why the recovery of leaf growth was incomplete, though P had fully recovered.

3) When water stressed plants were supplied with sufficient water, the leaf growth recovered only incompletely, because Ex recovered little while P recovered completely. The Ex was irreversibly reduced by water stress.

4) As mentioned above leaf growth was affected by both Ex and P, but the results obtained under various soil water regimes suggest that it is mainly regulated by Ex in most cases.

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〔和 文 摘 要〕

水不足に対するダイズの馴化

第3報 葉の生長の変化と，葉の“伸長性”，圧ポテンシャルとの関係

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ポット栽培したダイズ（品種農林2号）を用いて，葉の生長を葉の“伸長性”（葉片に錘りをかけたときの，葉片の単位時間あたりの伸び量，Ex）と，圧ポテンシャル（P）との両面から検討した．得られた結果の大要は，以下の通りである．

1) 給水を停止すると，土壌水分含量は低下し，それに伴ない葉の生長速度は低下して，土壌水分レベルが45%（対圃場容水量）に達したとき，葉の生長は完全に停止した．その後，土壌水分レベルを45%に保ったところ，葉は再び生長を始めた．このことから，葉の生長において乾燥への馴化がおこると考えられた．しかし，生長再開後の葉の生長速度は十分に給水した対照区（土壌水分レベル80%）の葉と比べて，小さかった．

2) 給水停止後，葉の生長速度が低下したときには，PとExの両者が共に減少した．その後Pは，対照区のレベルにまで回復し，このことが葉の生長の再開を可能にしたと考えられた．Pの回復は，浸透ポテンシャルの低下，すなわち浸透調節によりもたらされた．いっぽう，Exは，低い値にとどまり，回復しなかった．低水分状態が維持されたときに，Pが完全に回復するにもかかわらず，生長の回復が不完全な程度にとどまるのは，Exが低い値にとどまることによると考えられた．

3) 植物体を低水分下に置いた後，十分給水すると葉の生長は回復するが，対照区にはおよばなかった．乾燥処理後の再給水により，Pは十分回復したが，Exの回復は不十分であり，このことが，生長回復の不十分さの基礎となっていると考えられた．またこのことから，Pはその時々の条件に応じすみやかに変化しうるが，Exは低水分条件により，かなり不可逆的な減少をきたすようであった．

4) 本実験の結果の全体をみると，葉の生長速度は，P，Exの両者と正の相関を示したが，後者との間の相関のほうがより密接であった．