インゲンマメの光合成,蒸散及び水利用効率に及ぼす環境要因とSADH処理の影響

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The Effects of Environmental Factors and SADH on Photosynthesis, Transpiration, and Water Use Efficiency in Bean Plants

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Summary

To examine the effects of environmental factors and SADH(succinic acid 2,2-dimethylhydrazide) on water use efficiency (WUE), photosynthesis and transpiration of the primary leaf of bean plants were measured.

When light intesity, temperature, or water vapor santuration deficit was varied, WUE was not improved under the environmental conditions favorable for bean plants. Although some morphological modifications were observed in the SADH applied plant, the enhancement of WUE was not obtained.

Changes in the rate of photosynthesis and transpiration were observed during the development of the primary leaf, causing the change in WUE. In the younger leaf, WUE increased with aging. After reaching a peak when the leaf fully expanded, WUE decreased to the lowest value in the early reproductive stage. From these results, the possibilities of maintaining WUE at higher levels during the leaf development were discussed.

Key words: water use efficiency, environmental factor, growth retardant, leaf aging.

Introduction

There has been considerable interest to minimize the plant water requirement, especially in the crop production in the greenhouse or in arid land. Photosynthesis and transpiration are the plant functions that carbon dioxide and water are exchanged through the same pores of stomata. To obtain the high productivity of crop plants, it is required to keep photosynthetic rate at higher levels without increasing the transpiration rate. However, the observations that higher photosynthetic rate usually accompanied higher transpiration rate[2,3] make it uncertain whether these attempts are possible or not. Nevertheless, various works have been done to improve the effeciency of plant water use by the application of chemicals[7], improvement of management practices[1], or plant breeding[9,18,22].

In the preceding paper[19], we reported that drought tolerance of bean plants was enhanced by the application of a growth retardant (succinic acid 2,2-dimethylhydrazide, SADH). This effect was considered to be due to the morphological alterations in the leaf tissue and T/R ratio (Top/Root ratio), resulting in the increase of water-holding capasity of the plant. However, there has been little evidence which indicates that growth retardants reduce water loss through transpiration and enhance water use efficiency (WUE)[13].

Since it is expected that photosynthesis and transpiration change under the different environmental conditions and during the leaf development, experiments were designed to examine whether WUE can be altered by SADH application to the plant or by controlling environmental factors, and whether changes in WUE can be observed during the leaf development.

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Materials and Methods

Bean plants (*Phaseolus vulgaris* L. cv. Yamashiro Marusaya Kuro) planted in the black polyvinyl pot (9 cm in diameter) were grown in the phytotoron where temperature was controlled at 20℃ (day)—15℃ (night) in Experiment 1 and 25℃ (day)—20℃ (night) in Experiment 2 under natural light conditions. The soil and nutrient solution used in these experiments were prepared and SADH (succinic acid 2,2-dimethylhydrazide) was applied as described previously[19].

Photosynthesis and transpiration of the primary leaf were measured in the open system by using infra-red analyzers of CO_2 and H_2O, respectively. The measuring system was described in details in the preceding paper[19]. To control temperature in the assimilation chamber, temperature-controlled water was circulated in the stainless chamber. To control humidity in the chamber, the air saturated with water vapor at 20.3℃ and the air dried by passing through the refrigerator and $CaCl_2$ column were mixed by controlling the air flow rates. Water use efficiency (WUE) was calculated by dividing photosynthetic rate by transpiration rate and expressed as mg CO_2 / g H_2O.

In Experiment 1, the effect of environmental conditions in the assimilation chamber were examined by using the primary leaf of 7 to 19 days old plants. In the experiment of varied light intensity, 1-3 layers of black cheesecloth were placed on the assimilation chamber. Temperature and relative humidity were kept at 25℃ and 50%, respectively. In the experiment of varied temperatures, light intensity and saturation deficits were controlled at ca. 500 $\mu Em^{-2}s^{-1}$ and 16.85 mg H_2O/1, respectively. In the experiment of varied saturation deficits, temperature and light intensity were maintained at 25℃ and ca. 500 $\mu Em^{-2}s^{-1}$, respectively.

In Experiment 2, photosynthesis and transpiration of the primary leaf were measured for 38 days after sowing. Temperature, relative humidity, and light intensity were maintained at 25℃, 50%, and ca.500$\mu Em^{-2}s^{-1}$, respectively.

Results

Experiment 1

The effects of light intensity on photosynthesis and transpiration are shown in Fig.1. Photosynthesis increased with increasing light intensity in both control and SADH applied plants. At light intensities lower than ca.400 $\mu Em^{-2}s^{-1}$, no difference was found between control and SADH applied plants. In control plants, however, photosynthesis saturated at ca.400 $\mu Em^{-2}s^{-1}$, whereas in SADH applied plants its saturation was not found in this experiment and photosynthetic rate was relatively high at higher light intensities. Likewise, transpiration increased with increasing light intensity and at lower intensities, no differences in its rate were observed between control and SADH applied plants. At higher intensities, transpiration of SADH applied plants was higher than that of control plants. As shown in Fig.1, WUE was higher at lower light intensities at ca. 200 $\mu Em^{-2}s^{-1}$. However, a marked difference

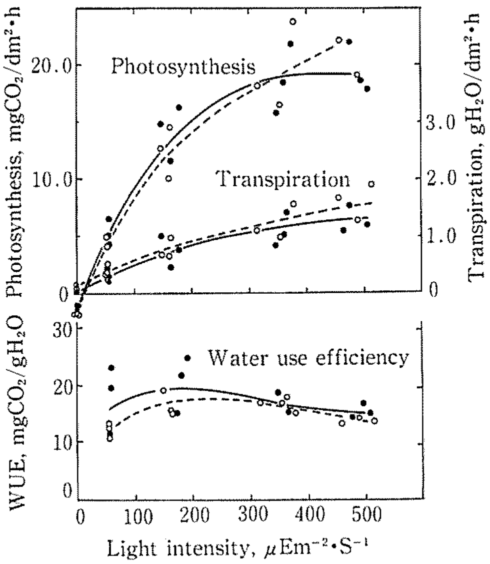
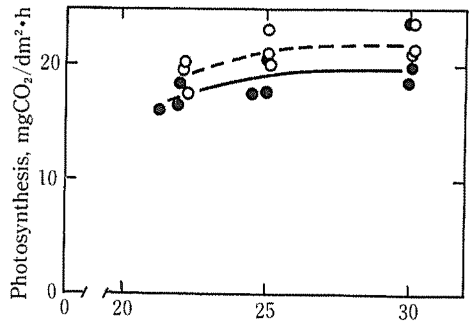
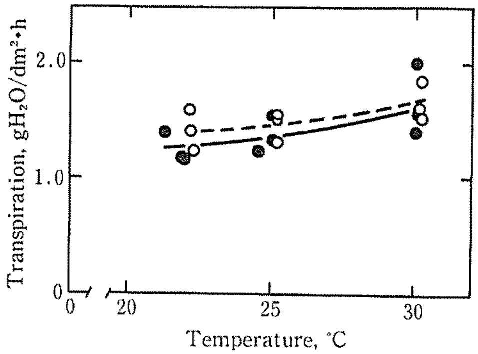


Fig. 1. The effect of light intensity on photosynthesis, transpiration, and water use efficiency. Closed circles and solid lines; control plants, open circles and broken lines; SADH applied plants.





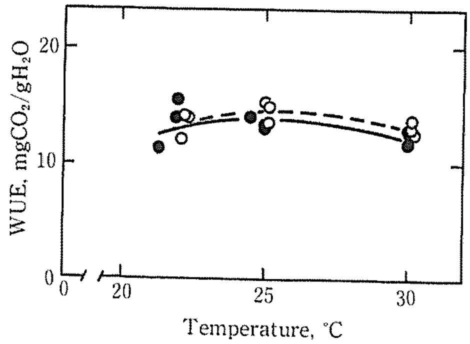
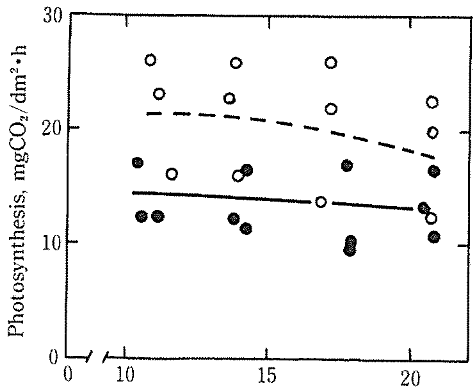
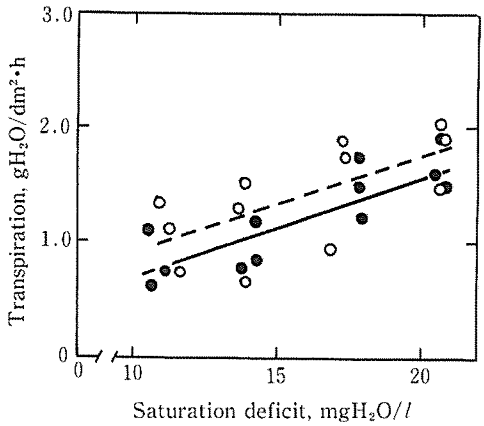


Fig. 2. The effect of temperature on photosynthesis, transpiration, and water use efficiency. Closed circles and solid lines; control plants, open circles and broken lines; SADH applied plants.





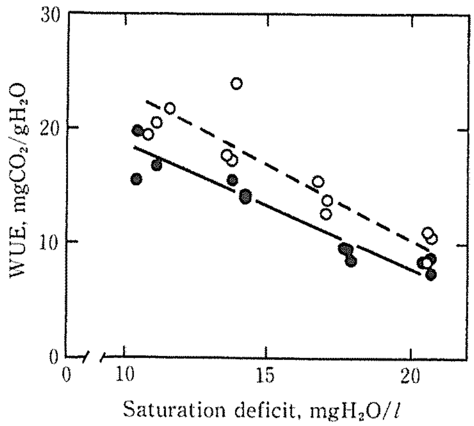


Fig. 3. The effect of saturation deficit on photosynthesis, transpiration, and water use efficiency. Closed circles and solid lines; control plants, open circles and broken circles; SADH applied plants.

was not obtained between control and SADH applied plants. The effect of temperature is shown in Fig.2. Within the range of temperatures examined in this experiment, photosynthesis, transpiration, and WUE were relatively constant. By the application of SADH, photosynthesis was slightly enhanced. However, SADH had no effect on transpiration and WUE. Photosynthesis slightly decreased and transpiration increased with increasing saturation deficits, being higher in SADH applied plants (Fig.3). These findings resulted in the decrease in WUE with increasing saturation deficits. WUE in SADH apllied plants was slightly higher. As shown in Fig.4, the oscillation in transpiration was observed in control plants. However, in SADH applied plants, the oscillation was not observed in the measurement even under the condition of the highest saturation deficit in this experiment.

Experiment 2

Changes in photosynthesis, transpiration, and WUE during the leaf development are shown in Fig.5. The primary leaf unfolded on the 7th day and fully expanded on the 14th day after sowing. Photosynthesis reached a maximum value slightly before the full expansion of the primary leaf and thereafter decreased. After the 28th day at the time of flowering in the terminal flower cluster, photosynthesis increased slightly. At the

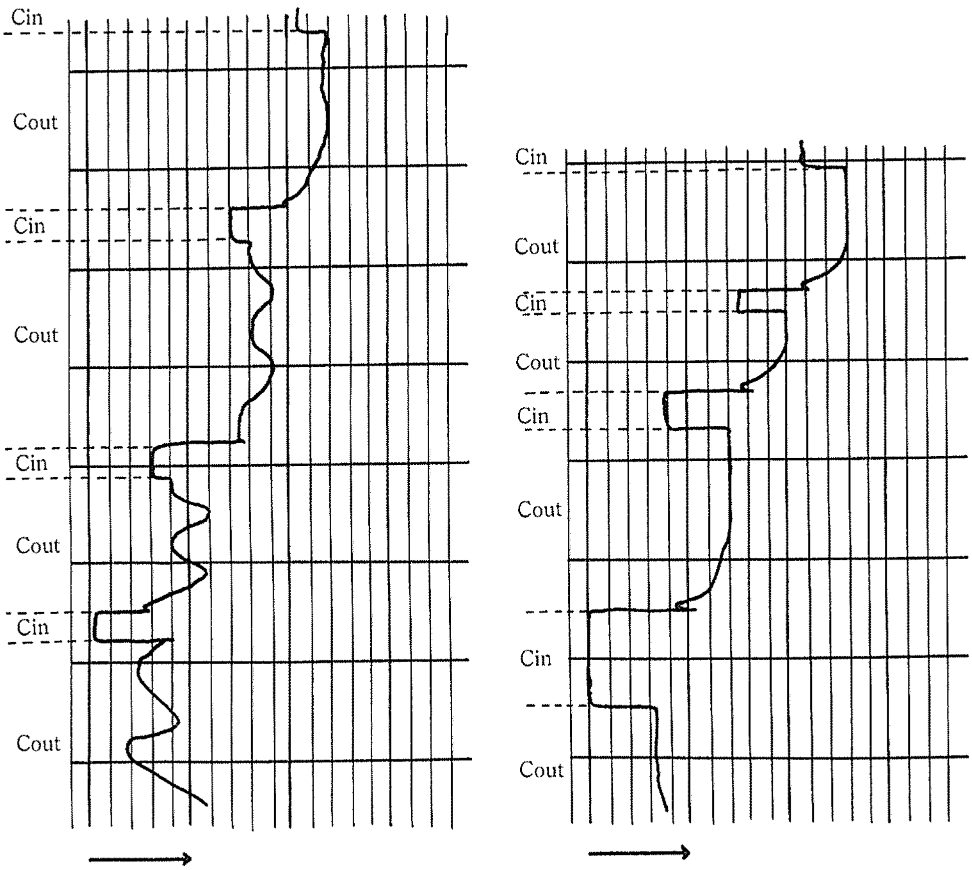


Fig. 4. Profiles of transpiration measurement in control (left) and SADH applied (right) plants. The direction of arrows indicates increasing water vapor. Water vapor concentration of the air at the inlet and the outlet of the chamber are indicated by C_{in} and C_{out}, respectively.

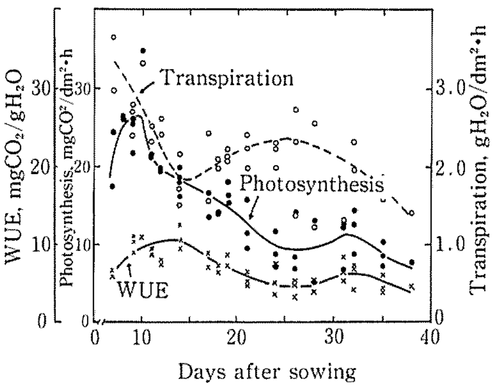


Fig. 5. Changes in photosynthesis, transpiration, and water use efficiency during the development of the primary leaf.

end of this experiment, photosynthesis decreased. WUE increased with aging and reached a peak on the 14th day at full expansion of the primary leaf, being followed by the decrease with the lowest WUE around the 25th day.

Discussions

Water use efficiency is expressed as mg CO_2 fixed by photosynthesis per g H_2O lost by transpiration. For the efficient water management, it is necessary to increase WUE. Attempts to increase photosynthesis without the increase in transpiration have been made by many workers[6,10]. However, in many cases, transpiration is high in the plant with high photosynthetic rate[2,3]. According to Fischer and Turner[6], WUE was defined as following equation :

$WUE = \Delta_c * D_c(r_a + r_s) / \Delta_e * D_e(r_a + r_s + r_i)$,

where

Δ_c and Δ_e are the leaf-to-air concentration differences of CO_2 and water vapor, respectively ; D_c and D_e the difusivities of CO_2 and water vapor, respectively ; and r_a, r_s and r_i the boundary layer, stomatal, and internal resistances to difusion, respectively. It is well recognized that photosynthesis and transpiration are affected by various environmental factors through their effects on the parameters in the equation. As shown in Fig. 1, photosynthesis and transpiration increased with increasing light intensity. Whereas, WUE increased at lower intensities, reached a peak at ca. $200\mu Em^{-2}s^{-1}$ and slightly decreased or was maintained at constant values at high intensities. It appears likely that a slightly higher increase in photosynthesis than in transpiration at lower intensities caused the increase in WUE. However, in the range of higher intensities in which photosynthetic rate is high, WUE was maintained at relatively constant value or slightly decreased. According to the theory expressed by the above equation, light intensity affects WUE through the effect on leaf temperature, r_s, and r_i. At lower intensities, WUE increases because of the decrease of r_s and r_i, while at higher intensities, WUE decreases because of the increase of r_s caused by the enhanced leaf temperature. Therefore, it is expected that there is an optimum light intensity for the maximum WUE. Light intensity ($500\mu Em^{-2}s^{-1}$) in this experiment appeared to be lower than the supra-optimum intensity, resulting in the constant WUE. Within the range of temperature of 20-30℃, changes in photosynthesis were very small, transpiration was constant or slightly decreased, and changes in WUE was not estimated(Fig.2). The influence of temperature on WUE is considered to be complicated. With increasing temperature, Δ_e increases and WUE decreases. At higher temperatures, r_s is expected to increase because of the increase in CO_2 concentration in the leaf by the enhanced respiration. On the other hand, r_i is considered to decrease by the enhancement of photosynthetic metabolism below the optimum temperature and to increase under the supra-optimum conditions. Therefore, in this experiment, it appeared likely that WUE was constant because the temperature condition was in the optimum range for bean plants. The saturation deficit is an important factor affecting Δ_e and WUE. As shown in Fig.3, transpiration increased linearly with increasing saturation deficit. Photosynthesis tended to be constant or slightly decrease at higher saturation deficits due to water stress. Accordingly, WUE decreased linearly with increase in saturation deficit. From these results, it was suggested that, under the conditions favorable for growth and photosynthesis of bean plants, WUE could not be improved by controlling environmental factors.

In the preceding paper[19], we reported that morphological modifications in the leaf tissue and T/R ratio were caused by SADH application and as a result the water-holding capacity increased. These effects of SADH enhanced drought tolerance under water stressed conditions. With regard to the effect of SADH on transpiration, it was reported that transpiration was slightly decreased in SADH applied apple leaves[13]. In this experiment, however, transpiration and photosynthesis tended to be enhanced by SADH application. According to Patterson et al[15], photosynthesis of thick leaves is high in the field-grown cotton plants. This phenomenon is partly explained by the increase in the surface area of mesophyll cells exposed to the intercellular space[5,41]. The other explanation may be proposed by the results as shown in Fig.1 ; at higher light temperatures, the saturation of photosynthesis was not observed in SADH applied plants. This phenomenon might be explained by the higher efficiency of light energy absorption in the thicker leaves. Although leaf temperature was not measured in this experiment, it is expected that leaf temperature enhanced by higher light intensities was below the range in which r_s increased by stomatal closure, because the light intensities were not too high (500 $\mu Em^{-2}s^{-1}$). On the other hand, stomatal size and density are also important factors affecting transpiration. However, our unpublished results show that they were not affected by SADH application ; stomatal sizes in control and SADH applied plants were 26.9μ and 28.1μ in length, respectively, and stomatal densities were 4900 and 5000/cm^2, respectively. From these facts, it is also expected that transpiration is enhanced in thicker leaves, as already reported in *Ficus benjamina* plants[4]. Another point of view is considered to be related with the higher transpiration stream in SADH applied leaf because of the increase in capillary attraction of fine xylem vessels (unpublished). However, the rate of enhancement in photosynthesis and transpiration by SADH application was mostly equal, except for the experiment of saturation deficits in which a marked enhancement of photosynthesis by SADH application was obtained as compared with the result shown in Fig.1 and Fig.2. The reason for this phenomenon is not clear in this experiment. From the results obtained in these experiments, it is supposed to be difficult to increase WUE by SADH application.

It is also well recognized that photosynthesis and transpiration change during the leaf development. As shown in Fig.5, both of photosynthesis and transpiration were high in the younger leaves and low in the older leaves. Furthermore, no parallel change was observed between photosynthesis and transpiration, resulting in the change in WUE during the leaf development. In the younger leaf which is not fully expanded, transpiration was very high. In this stage, photosynthesis was still low and reached a peak slightly before full expansion of the leaf. The decrease in transpiration was observed with leaf age, followed by a slight increase around the 17th day. Thereafter transpirstion was maintained at constant value when the development of flower buds has started. Flowering was observed in the terminal flower cluster on the 28th day. The same finding were reported in cucumber plants[8,12], suggesting that transpiration increased in the early stage of reproductive growth. The decline in photosynthesis was observed after its peak, followed by the slight increase around the 30th day at the stage of flowering and the growth of young pods. The same findings were also reported in soybeans[11,16] and the other plants[17,20,21] and explained by the stimulation of photosynthesis caused by the increase in the sink demand. Accordingly, WUE increased during the young leaf stage and reached a peak around the 14th day and thereafter decreased. From these results, the highest WUE is suggested to be obtained in the stage of full expansion of the leaf and the lowest WUE in the reproductive stage of bean plants. The regulation of stomatal closure is supposed to be defective at that stage. If the increase in transpiration in the reproductive stage can be prevented by some means or other, WUE can be maintained at higher levels throughout the development of the primary leaf in beans. During the leaf development, r_a, r_s, and r_l are expected to change. Further experiment is necessary to clarify the mechanism of the increase of transpiration in the reproduction stage.

As shown in Fig.4, oscillation in transpiration was observed under the conditions of higher saturation deficits in control but not in SADH applied plants. The oscillation appeared to be caused by a marked stomatal movement during the measurement. Under the conditions of high saturation deficits, transpiration is accelerated and a large amount of water is lost from the leaf because of the larger Δ_e. As shown in the preceding paper[19], the enhancement of water-holding capacity in SADH applied plants was suggested to be caused by the increase in leaf thickness, resulting in the succesive water supply to the site of transpiration. In this experiment, high water-holding capacity is also supposed to prevent stomatal closure in SADH applied plants under the conditions of higher evaporative demand.

Conclusively, WUE could not improved by controlling the environmental factors being in the range optimal for bean plants and by SADH application. However, it was reconfirmed that, in SADH applied plants, higher water-holding capacity may play an important role against the increased water loss under the severely dried conditions. Furthermore, the possibility that WUE is maintained at higher levels during leaf aging can be foreseen if the increase in transpiration in the reproductive stage can be prevented.

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インゲンマメの光合成，蒸散及び水利用効率に及ぼす環境要因とSADH処理の影響

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作物の水利用効率 (WUE) を高める技術を開発するための基礎的知見を得るために，インゲンマメを用いて光合成，蒸散及び WUE に及ぼす環境要因と SADH (Succinic acid 2,2-dimethylhydrazide) 処理の影響を調べた．

光強度，温度及び飽差により WUE は変化したが，インゲンマメの生育に好適と思われる条件下では，SADH 処理により WUE は高めることはできなかった．初生葉の発育に伴い光合成と蒸散は変化し，WUE は葉面積が最大に達する頃に最も高くなった．以後，加齢に伴い低下した．この WUE の低下には，生殖成長開始期から蒸散の増大が強く影響しているものと考えられた．したがって，この時期の蒸散の増大の機構を明らかにすることが，葉の WUE を生育時期を通して高く維持させる技術を開発するために重要と考えられた．

(園芸学研究室)