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# Varietal Differences in Flowering, Pod Setting and Photosynthesis in Soybean Under High Temperature Conditions

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## Abstract

High temperatures, due to global warming, is an increasing environmental stress that influences soybean (*Glycine max* (L.) Merr.) growth and yield breeding tolerant cultivars for high temperature conditions is of high importance. This experiment was conducted to evaluate the varietal differences of soybean photosynthetic apparatus and agricultural characteristics, such as flowering, pod number, and yield under high temperature conditions. Seven cultivars were selected from the world soybean core collection, which were derived from the Genebank Project, National Agriculture and Food Research Organization in Japan, and 2 Japanese cultivars were used and grown in greenhouses. The high temperature (HT) treatment delayed the beginning pod and full maturity stages by 1 to 10 days and -1 to 17 days, respectively. Flower number per plant had a tendency to become larger in the HT treatment when compared to that of the control in the HT treatment, pod setting rates decreased and then seed number decreased, which resulted in a decrease in yield, but flower number increased. The decrease in pod number depended mainly on the decrease in pod setting rate. The actual quantum yield of Photosystem II (PSII) ($\Phi_{PSII}$) was not different between the control and HT treatment, indicating the HT treatment did not reduce the efficiency of electron transport in the PSII for any of the cultivars. The maximum quantum yield of PSII (Fv/Fm) did not show a significant difference between the control and the treatment groups. Every plot was more than 0.79, and we assumed no photoinhibition occurred in the HT treatment. The degree of heat dissipation in PSII was similar in both the control and the treatment groups and among the cultivars. The $CO_2$ assimilation rate ($A_N$) had a close relationship with stomatal conductance ($g_s$) in the control and treatments groups, indicating that a cultivar with a high stomatal conductance had a tendency for high $CO_2$ assimilation rate. The other photosynthetic characteristics did not show a relationship with $A_N$. There was no significant decrease in Fv/Fm in the HT treatment when compared to that of the control in this experiment. The photosynthetic apparatus may have not been damaged by the HT treatment in this experiment. A higher transpiration ability in soybean may be associated with a higher adaptability for high temperature conditions.

**Keywords:** $CO_2$ assimilation rate; Chlorophyll fluorescence; High temperature; Flowering number; Pod number; Pod setting; Transpiration rate; Seed yield; Soybean

## Introduction

Under nearly all scenarios, global surface temperature is likely to exceed 1.5°C relative to 1850-1900 at the end of the 21st century [1]. Lobell and Asner [2] predicted that soybean yield in the US will decrease by roughly 17% with a 1°C increase in the growing season temperature. In northeast China, soybean yields have declined significantly due to warming trends since 1987 [3]. Experimental studies show that high temperatures cause several negative effects on soybean growth and/or yield seed yield was slightly reduced by high temperature stress when induced only during the initial seed filling period [4]. An increase in temperature decreased seed weight, which was mainly due to a reduction in seed size [5]. Total dry matter, seed yield, and harvest index were reduced by an increase in temperature when using a temperature gradient chamber [6]. Pollen morphology and viability were also negatively affected by high temperatures [7], which resulted in a lower pod-set and seed weight concomitant with a decreased photosynthetic rate [8].

Several commercial heat tolerant cultivars of rice have been released in Japan [9], and others are being developed in the IRRI [10], Vietnam [11], and Bangladesh [12]. Heat-tolerant genotypes of potato have also been developed [13]. For soybean, however, heat tolerant breeding projects are yet to be undertaken, although genes related to heat tolerance have been explored [14]. In addition to such exploration, it is important to evaluate the phenotypic avoidance and/or adaptation mechanisms of heat tolerance in the photosynthetic apparatus and other agronomic characteristics However, only few studies have been conducted on the varietal differences in such characteristics, despite being the essential information for breeding. Therefore, the varietal differences for phenotypic characteristics associated with heat tolerance in soybean should be evaluated.

Photosynthesis is a key phenomenon that substantially contributes to crop yield [15]. There have been reviews on $CO_2$ gas exchange characteristics; however, several studies suggest that photosynthetic rate could be used as a potential indicator of heat tolerance, while other studies report little to no association of this physiological trait with heat tolerance. This may be because of the variation in photosynthetic capacity for different species under varying degrees of stress tolerance. In soybean, there are only a few studies about photosynthesis under heat stress conditions [16-18]; therefore, it is necessary to evaluate $CO_2$ assimilation rates ($A_N$) under heat stress

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conditions. In addition to $A_N$, transpiration is one of the main factors for avoiding heat stress [19]. It has been shown that the differences between soybean and cotton adaptation mechanisms in arid conditions depend on transpiration ability.

Chlorophyll fluorescence measurements are commonly used to study the functions of the photosynthetic apparatus [20,21]. In particular, the maximum quantum yield of photosystem II (PSII) (Fv/Fm) is used as a sensitive indicator of photosynthetic performance, such as photoinhibition [21]. In addition to Fv/Fm, actual quantum yield of PSII ($\Phi_{PSII}$) and $qN$ are also evaluated for the efficiency of PSII photochemistry and non-photochemical quenching, respectively, to evaluate their relationship with heat dissipation of excessive energy [21]. In this experiment, we evaluated the varietal differences of physiological characteristics, including photosynthetic apparatus, and agricultural characteristics, including flowering, pod number, and yield under high temperature conditions.

## Materials and Methods

During the year previous to this experiment, 80 cultivars from the world soybean core collection, which were derived from the Genebank Project, National Agriculture and Food Research Organization in Japan, were grown in greenhouse conditions, then 7 cultivars were selected with the following criteria: beginning flowering (R1) was from August 10-13, stem height was less than 80 cm, under the conditions in Matsudo, Chiba, Japan (lat 36″N, long 140″E). In addition to these 7 cultivars, 2 Japanese cultivars, Enrei and Tachinagaha, were used in this experiment (Table 1).

| Cultivar | Origin |
|---|---|
| Enrei | Japan |
| Tachinagaha | Japan |
| Chunhoku 2 | Rep Korea |
| Shirosota | Korean Peninsula |
| Chieneum Kong | Rep Korea |
| Kongnamul Kong | Rep Korea |
| Heukdaelip | Rep Korea |
| Heamnam | Rep Korea |
| Uronkon | Korean Peninsula |

**Table 1:** Materials.

The experiment was conducted in two greenhouses at the Faculty of Horticulture, Chiba University in 2015. Six pots were used for each treatment for a single cultivar. Three seeds were sown in a 1/5000 Wagner pot (height 198 cm, average diameter 16 cm) on June 24 and were thinned to one plant per pot after emergence. The plants were grown in the open air before the beginning of flowering (R1), after which two air temperature treatments were used starting on August 6. The pots in the high temperature (HT) experiment and the control were grown in the greenhouses. The HT treatment had a maximum air temperature of 41°C and was controlled by opening the windows of the greenhouse; the control group had an air temperature similar to the ambient temperature and was controlled by maintaining open windows. The mean difference of the daily mean air temperature between the HT and the control group was 0.95°C during the experimental period. After R1, flower number and flowering period were measured daily for every pot. The pots were irrigated up to 2-3 times a day, according to the soil conditions. At the harvesting time, 3 pots per treatment for a cultivar were harvested individually, and the yield and yield components were measured. Seed yield was determined after oven drying at 80°C for 72 h. The rates of yield and yield components were calculated as follows: (the control-the treatment)/the control.

Chlorophyll fluorescence parameters including the quantum yield of Photosystem II (PSII)($\Phi_{PSII}$), maximum quantum yield of PSII (Fv/Fm), and non-photochemical quenching ($qN$) were measured for the Chieneum Kong, Chuuhoku 2, Tachinagaha, and Uronkon cultivars by using a chlorophyll fluorometer (PAM-2000, Waltz, Germany) on August 18. $CO_2$ assimilation rate ($A_N$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$), and transpiration rate (E) for Chuuhoku 2, Tachinagaha, and Uronkon were also measured using a portable photosynthesis system (LI-6400, Li-Cor, USA) on August 21. The uppermost fully expanded leaves were used for the measurement from 0900 to 1400 h.

## Results

### Flowering period and number and pod number and setting rate

The growth stages for each cultivar are shown in Table 2. The HT group showed delayed growth stages. The HT group showed a delay in the beginning pod and the full maturity stages by 1 to 10 days and -1 to 17 days, respectively.

| Cultivar | Growth stage | | | | |
|---|---|---|---|---|---|
| | R1 | R3 | | R8 | |
| | | Control | HT | Control | HT |
| Enrei | 31 Jul | 11 Aug | 12 Aug | 5 Oct | 9 Oct |
| Tachinagaha | 31 Jul | 11 Aug | 12 Aug | 25 Oct | 6 Nov |
| Chunhoku 2 | 3 Aug | 9 Aug | 18 Aug | 11 Oct | 19 Oct |
| Shirosota | 3 Aug | 9 Aug | 14 Aug | 25 Oct | 25 Oct |
| Chieneum Kong | 3 Aug | 10 Aug | 15 Aug | 9 Oct | 8 Oct |
| Kongnamul Kong | 3 Aug | 10 Aug | 18 Aug | 24 Oct | 4 Nov |
| Heukdaelip | 4 Aug | 10 Aug | 16 Aug | 26 Oct | 12 Nov |
| Heamnam | 5 Aug | 10 Aug | 13 Aug | 24 Oct | 29 Oct |
| Uronkon | 5 Aug | 18 Aug | 28 Aug | 26 Oct | 5 Nov |

**Table 2:** Growth stages (R1, R3 and R8) of each cultivar in the control and high temperature treatment (HT). R1: Beginning flowering stage, R3: Beginning pod stage and R8: Full maturity stage.

Table 3 shows flower number, pod number, and pod setting rate the flower number per plant tended to be higher in the HT group than in the control Kongnamul Kong, Heukdaelip, and Uronkon showed significantly more flower numbers in the treated group than in the control.

| **Cultivar** | **Flower Number (plant$^{-1}$)** | | | **Pod Number (plant$^{-1}$)** | | | **Pod Setting Rate (%)** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Control** | **HT** | | **Control** | **HT** | | **Control** | **HT** | |
| Enrei | 105c | 121d | ns | 49c | 43cd | ns | 49a | 36a | ns |
| Tachinagaha | 112c | 132d | ns | 22d | 38cd | ns | 20de | 28ab | ns |
| Chunhoku 2 | 289a | 360ab | ns | 145a | 115a | ns | 50a | 33a | * |
| Shirosota | 174bc | 198cd | ns | 55c | 55bcd | ns | 32c | 28ab | ns |
| Chieneum Kong | 280a | 335ab | ns | 81b | 64bc | ns | 30cd | 19bc | * |
| Kongnamul Kong | 216ab | 275bc | * | 89b | 92ab | ns | 41ab | 34a | ns |
| Heukdaelip | 159bc | 293abc | * | 54c | 21d | ns | 36bc | 7d | * |
| Heamnam | 219ab | 251bcd | ns | 56c | 74bc | * | 26cde | 29a | ns |
| Uronkon | 282a | 407a | * | 52c | 67bc | ns | 18e | 17cd | ns |

**Table 3:** Flower number, pod number and pod setting rate affected by high temperature. Values in each column followed by the same letter are not significantly different at 5% level by LSD. * and ns indicate 5% level of significance and no significance between the control and high temperature treatment (HT), respectively.

There was no incremental increase in pod number for the HT group compared to the control. Only Heamnam showed a significant increase in the treatment group compared to the control. Pod setting rate showed a decreasing tendency in the HT group compared to the control. Chunhoku 2, Chieneum Kong, and Heukdaelip had a significantly lower pod setting percentage in the HT treatment than in the control. However, Enrei, Tachinagaha, Chunkoku 2, Shirosota, Kongnamul Kong, and Heamnam showed 30% for pod setting even in the treatment groups. Conversely, Heukdaelip showed a lower pod setting percentage in the HT treatment than in the control.

## Seed number, 100 seed weight, and yield

There was no significant difference between the control and the treatment groups for seed number, except for Heukdaelip. Most of the cultivars had a lower number of seeds in the treatment group than in the control group, but the other cultivars, including Shirosota, Kongnamul Kong, Heamnam, and Uronkon, had a larger number of seeds in the treatment group in the control groups (Table 4). Only the Heukdaelip cultivar showed a significant decrease in the HT treatment compared to the control. Every cultivar showed a significant decrease in 100 seed weight in the treatment group compared to the control, although Kongnamul Kong had a relatively larger seed size in the treatment group than in the control. Seed yield showed a decreasing trend in the HT treatment when compared to the control; Enrei, Chieneum Kong, and Heukdaelip had significantly smaller seed yields in the treatment than in the control. Conversely, Kongnamul Kong, Heamnam, and Uronkon showed a smaller decrease and a relatively higher yield in the HT treatment than in the control. There was no significant correlation between yield and the yield components.

| **Cultivar** | **Seed Number (plant$^{-1}$)** | | | **100 Seed Weight (g)** | | | **Yield (g plant$^{-1}$)** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Control** | **HT** | | **Control** | **HT** | | **Control** | **HT** | |
| Enrei | 91d | 67cd | ns | 27c | 20c | * | 24ab | 13cd | * |
| Tachinagaha | 60d | 50d | ns | 33a | 28a | * | 20b | 14cd | ns |
| Chunhoku 2 | 265a | 211a | ns | 10e | 8f | ** | 25ab | 16bc | ns |
| Shirosota | 75d | 84cd | ns | 29bc | 19c | ** | 21ab | 16bc | ns |
| Chieneum Kong | 137bc | 123bc | ns | 14d | 10e | * | 20b | 12cd | * |
| Kongnamul Kong | 146b | 165ab | ns | 15d | 14d | * | 23ab | 23a | ns |
| Heukdaelip | 97cd | 31d | * | 30abc | 25b | * | 29a | 8d | * |
| Heamnam | 86d | 102bcd | ns | 28c | 21c | * | 24ab | 21ab | ns |
| Uronkon | 81d | 95cd | ns | 32ab | 23b | ** | 26ab | 22ab | ns |

**Table 4:** Yield and yield components affected by high temperature. Values in each column followed by the same letter are not significantly different at 5% level by LSD. *, ** and ns indicate 5%, 1% level of significance and no significance between the control and high temperature treatment (HT), respectively.

Table 5 shows the correlation coefficients among the decreasing rate of yield and the yield components in the HT treatment [(the control-HT plot)/the control]. There was a highly significant correlation between yield and seed number, indicating the decrease in yield was caused mainly by the decrease in seed number. Yield also showed positive correlations with pod number and pod setting rate, although these values were not significant. The decrease in pod setting rate resulted in a reduced pod number increasing flower number in the HT treatment resulted in a reduction of pod setting rate.

| | **Flower Number** | **Pod Number** | **Pod Setting Rate** | **Seed Number** | **Seed Weight** |
|---|---|---|---|---|---|
| Yield | -0.53 | 0.62 | 0.63 | 0.92** | 0.14 |
| Flower Number | | -0.54 | -0.67* | -0.63 | 0.26 |
| Pod Number | | | 0.99** | 0.61 | 0.06 |
| Pod Setting Rate | | | | 0.64 | 0.01 |
| Seed Number | | | | | -0.25 |

**Table 5:** Correlation coefficients of decreasing rates of yield with yield components by high temperature. * and ** indicate 5% and 1% level of significance (n=9).

## Photosynthetic characteristics

Figure 1 shows the $CO_2$ assimilation rate ($A_N$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration rate ($C_i$), and the transpiration rate (E). There was no significant difference in $A_N$ between the treatments, however, Tachinagaha and Chunhoku 2 had a smaller $A_N$ in the HT treatment than in the control. There was no significant difference in $g_s$ between the control and the HT treatment, although higher values were noted in Chunkuku 2 than in the other two cultivars. Chunhoku 2 and Uronkon showed no significant difference in $C_i$ between the control and the treatment; however, Tachinagaha had a smaller $C_i$ value in the control than in the HT treatment. The HT treatment had higher E values for every cultivar than those of the control, where Chunboku 2 had the highest values followed by Uronkon.

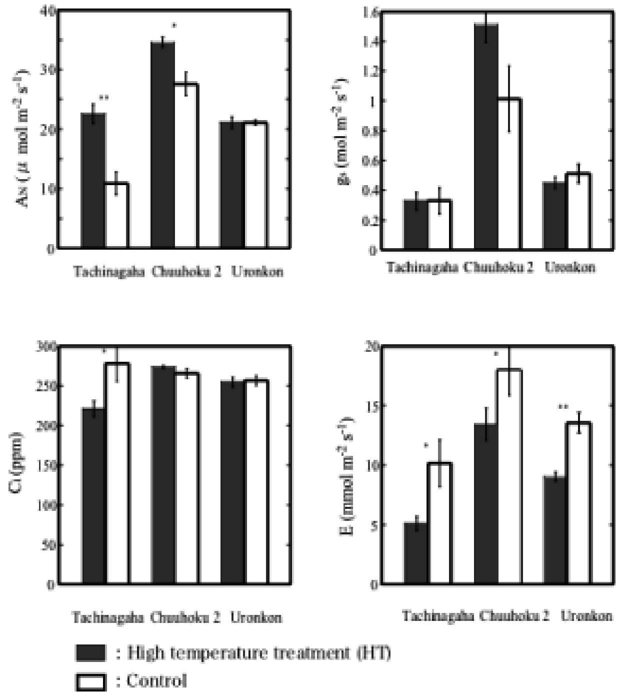

**Figure 1:** Effects of high temperature on $CO_2$ assimilation rate ($A_N$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration rate ($C_i$) and transpiration rate (E) for Tachinagaha, Chunhoku 2 and Uronkon. Bars indicate standard errors. *, ** indicate a significant difference between the control and high temperature treatment (HT) at 5% and 1% level, respectively.

The actual quantum yield of PSII ($\Phi_{PSII}$) was not significantly different between the control and the HT treatment, indicating that high temperature did not reduce the efficiency of electron transport in PSII in any of the cultivars. There was no varietal difference in $\Phi_{PSII}$. The maximum quantum yield of PSII was not significantly different between the control and treatment groups. Every plot had more than 0.79, assuming there was no photoinhibition by the HT treatment. There was also no significant difference in *qN* between the control and treatment groups. The degree of heat dissipation in PSII was similar in both the control and HT groups and among the cultivars.

Figure 2 shows the relationships of $A_N$ to $g_s$, $C_i$, E, $\Phi_{PSII}$, Fv/Fm, and *qN*. The $A_N$ was closely related to $g_s$ in both the control and HT treatments, indicating that cultivars with a high stomatal conductance tend to have a high $CO_2$ assimilation rate. The Chunboku 2 cultivar in both the control and treatment groups showed high $A_N$ value because of the high $g_s$ in both the groups. The other photosynthetic characteristics did not show a relationship with $A_N$.

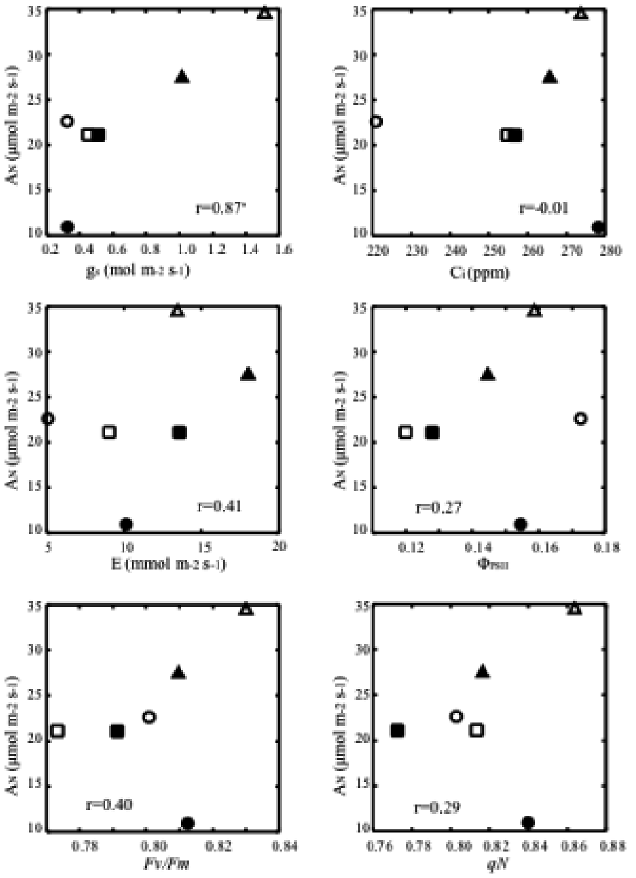

**Figure 2:** Relations of $CO_2$ assimilation rate ($A_N$) to stomatal conductance ($g_s$), intercellular $CO_2$ concentration rate ($C_i$), transpiration rate (E), actual quantum yield of PSII ($\Phi_{PSII}$), maximum quantum yield of PSII (Fv/Fm) and *qN*. Open and closed symbols are the controls and high temperature treatments, respectively. ○, △ and □ indicate Tachinagaha, Chunboku 2 and Uronkon, respectively. * indicates 5% level of significance.

## Discussion

The HT treatments in this experiment showed decreased pod setting rates and then decreased seed number, which resulted in a decrease in yield and an increase in flower number. The decrease in yield from the HT treatment was caused mainly by the decrease in seed number, which was followed by a decrease in pod number and pod setting rate. The decrease in pod number depended mainly on the decrease in pod setting rate. The seed set rate primarily depended upon the function of pollen and the ovule, successful pollination, fertilization, and post-fertilization processes [8]. For soybean, studies have shown that pollen viability and germination decreases with high temperatures [8,22]. Conversely, it has also been reported that there is a decreased amount of assimilates available for growth due to high respiration rates associated with pod setting rates rather than due to pollen viability [23]. In this experiment, some cultivars, including Kongnamul Kong, Heamnam, and Uronkon, showed a small decrease in yield, even under the HT treatment. The pod setting rates in the HT treatment were not significantly different from those in the control. These cultivars might, therefore, have a low effect on pollen viability and decreased amounts of assimilates even under the HT treatment. Conversely, the cultivars with significantly low pod setting rates, including Heukdaelip and Chunhoku 2, might have low pollen viability and/or excessive consumption of assimilates due to respiration in the HT treatment.

The sustained decrease in Fv/Fm indicates the occurrence of photo-inhibitory damage in response to one or more environmental stresses [21]. There was no significant decrease in Fv/Fm in the HT treatment compared to the control, and the photosynthetic apparatus may have not been damaged by the HT treatment in this experiment. Inamullah and Isoda [24] compared soybean and cotton under water stress and high temperature conditions and reported that the photosynthetic apparatus in soybean was protected from photoinhibition under water stress because of its high ability to down-regulate PSII activity and activate xanthophyll cycle pigment conversion to dissipate excess excitation energy as heat. In this experiment, however, there was no significant difference between the actual quantum yield and *qN*, i.e., no marked down-regulation of PSII and heat dissipation in the HT treatment when compared to that of the control (Figure 3).

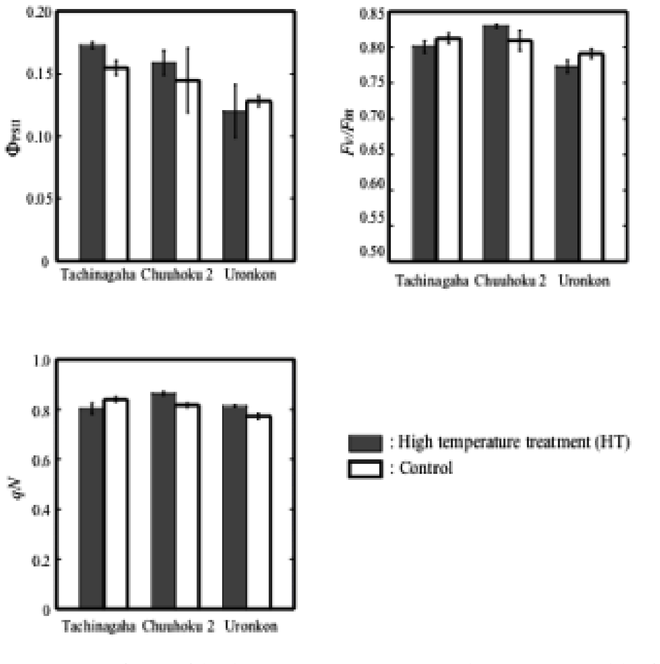

**Figure 3:** Effects of high temperature on actual quantum yield of PSII ($\Phi_{PSII}$), maximum quantum yield of PSII (Fv/Fm) and *qN*. Bars indicate standard errors.

Therefore, the carbon reactions of photosynthesis might not be largely affected by the efficiency of light reactions in this experiment. The decrease in $A_N$ by the HT treatment when compared to that of the control was observed in Tachinagaha and Chunhoku 2 compared to the control. In the HT treatment, Chunhoku 2 showed a decrease in $g_s$ but no decrease in $C_i$, while Tachinagaha showed no decrease in $g_s$ and an increase in $C_i$. It is, therefore, assumed that the main factor in the decrease of $A_N$ in Chunkoku 2 is $g_s$, and the decrease of $A_N$ in Tachinagaha is caused by something different. The high $CO_2$ concentration in the leaf with a low $CO_2$ assimilation rate in Tachinagaha indicates low rubisco activity. Uronkon had no significant decrease in $A_N$ in the HT treatment compared to the control. Isoda et al. [25] reported that leaf temperature in soybean was regulated by the combination of leaf movement and transpiration. Some cultivars regulated leaf temperature mainly through leaf para-heliotropic movement, whereas others by both transpiration and leaf movement. In this experiment, transpiration rates increased in the HT treatment group compared to the control. The cultivars used in the HT treatment might, therefore, regulate leaf temperature by transpiration, especially for Uronkon that showed an increase of E in the HT treatment compared to the control, which resulted in the prevention of photoinhibition and no decrease in $A_N$. Wang et al. [26] reported varietal differences in the transpiration ability of cotton and suggested that a cultivar with higher transpiration ability tended to have higher dry matter production in arid conditions. Therefore, we can assume that a higher transpiration ability in soybean may be also associated with a higher adaptability for high temperature conditions.

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