Changes in Thermotolerance of Photosynthetic Apparatus in Cucumber Leaves in Response to Water Stress and Exogenous ABA Treatments

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Summary

Effects of water stress and exogenous abscisic acid (ABA) treatments on thermotolerance of photosynthetic apparatus (PA) in cucumber (*Cucumis sativus* L.) leaves were investigated. Evaluation of thermotolerance was based on the heat sensitivity of photosystem II (PSII) based on chlorophyll fluorescence emission. Plants were water-stressed by either withholding water to intact plants or placing excised shoots in an open atmosphere in a glasshouse. The extent of water stress was monitored by measuring the water potential of leaves. At intervals during water stress treatment, the ratio of variable to maximum fluorescence (F_v/F_m) of leaves was determined. Immediately after that, the leaves were dipped in a water bath held at 45 °C for 10 min and F_v/F_m values were determined again. Percentages of F_v/F_m values remaining after the heat treatment were used as a measure of thermotolerance of PA. With intact plants, thermotolerance of PA increased significantly when the leaf water potential was decreased to -1.0 MPa; it attained maximum at -1.5 to -2.0 MPa. However, the thermotolerance decreased when water potential was further lowered to -4.0 MPa. Leaves of excised shoots showed similar changes in thermotolerance of PA in response to the decrease in water potential, except that the maximum tolerance was obtained at -0.8 MPa. When intact plants were re-irrigated after 3 days of water stress treatment, the thermotolerance of PA increased temporarily during the first 2 hr, and then decreased sharply within 24 hr to the level of the irrigated control plant leaves. Exogenous ABA applied to leaves of irrigated plants caused an increase in thermotolerance of PA depending on its concentrations. Leaves treated with 1.00 mM ABA showed nearly complete tolerance of PA within a day; this high tolerance level was maintained for at least 6 days. Leaves treated with 0.01 to 0.25 mM ABA reached a peak tolerance after a day and then lost much of the ABA-induced thermotolerance after 3 days. The results indicate that the enhanced thermotolerance of PA in water-stressed cucumber leaves was probably mediated through a water-stress-induced increase in endogenous levels of ABA.

Introduction

Under high temperature conditions, plants are usually exposed not only to heat stress but also to water stress. Water deficit in plant tissues may cause an increase in leaf temperature due to decreased transpiration. For this reason, water-stressed plants exhibit more severe injury on leaves when exposed to high air temperature (Oda et al., 1993). However, water stress that occurs prior to

high temperature stress has been reported to induce thermotolerance in maize leaves (Bonham-Smith et al., 1987). We also found that drought treatment before high temperature exposure increased thermotolerance of cucumber leaves (unpublished). In addition, water stress can induce chilling and freezing tolerances in many plant species (Utsunomiya, 1988). It appears that there is a common water-stress-related physiological mechanism by which the plants survive exposure to these stresses.

In general, plants accumulate abscisic acid (ABA) when exposed to stressful environments including

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drought (Cornic and Zeevaart, 1984), chilling (Chen et al., 1983), high temperature (Abass and Rajashekar, 1993), salinity (Talanova and Titov, 1994), and flooding (Zhang and Zhang, 1994). Furthermore, application of exogenous ABA enhances plant tolerance to various stresses (Robertson et al., 1994; Chen and Gusta, 1983). Based on these results, ABA is regarded as a general endogenous inducer of tolerance to environmental stresses (Mantyla et al., 1995).

Heat stress, depending on the temperature and duration, affects numerous physiological processes in plants. Moderately elevated temperatures diminish photosynthetic activities, accelerate senescence, and disturb respiration and movements of water and ion in cells (Camp et al., 1982). Extremely high temperatures can cause proteins to denature and degrade and disrupt cell membrane functions, e.g. leakage of cytoplasmic solutes. Photosynthetic apparatus (PA) is the primary target of high temperature stress (Berry and Björkman, 1980; Volger and Santarius, 1981). Photosystem II (PSII) reaction centers are very sensitive to heat and the activity of electron transport through them is inhibited at relatively moderate temperatures (Havaux, 1993). Although water stress can directly affect photosynthetic activity, PSII is not sensitive to water deficit (Cornic and Briantais, 1991). Results of He et al. (1995) show that water stress declined the steady state levels of major PSII proteins, but did not affect electron donation to PSII. It seems possible that the alteration in protein metabolism in PA or cells by water stress changes the heat sensitivity of the PA. However, there is no direct evidence in the literature on the thermal response of PA in water-stressed leaves and whether the thermotolerance of PA is controlled by ABA.

In the present study, we investigated the effects of water stress and exogenous ABA treatments on thermotolerance of PA in cucumber leaves. Evaluation of thermotolerance was based on chlorophyll fluorescence measurement, which has been shown as a reliable, rapid and non-destructive for detecting heat stress damage to PA or PSII (Smillie and Hetherington, 1983).

Materials and Methods

Experiment 1

Seeds of cucumber (*Cucumis sativus* L.) cv.

Nankyoku No. 2 were germinated on moist filter paper at 28 °C for a day. The seedlings were then planted individually in 350 ml plastic pots containing a mixture of bark compost and soil (1 : 3, v/v), and grown in a glasshouse kept at a maximum of 31.2 ± 3.2 °C (Tmax) and a minimum of 14.4 ± 1.4 °C (Tmin), with a mean solar radiation (SR) of 10.3 ± 5.8 MJ/m²/day during March to May. Four weeks after planting, plants with 3 fully expanded leaves were water-stressed by withholding water (0 ml/plant/day). Control plants were thoroughly irrigated daily (75–100 ml/plant/day). Chlorophyll fluorescence and water potential of leaves were measured by the methods as described below; at 1-day intervals for water-stressed plants and at 2-day intervals for control plants after treatment. Four plants were used per measurement.

Experiment 2

Plants were grown as in Experiment 1. Seven weeks after planting, roots of plants with 6 fully expanded leaves were excised below cotyledons and the shoots were water-stressed by placing them in the glasshouse to dehydrate. Chlorophyll fluorescence and water potential of the leaves of excised shoots were measured at 0, 2, 4, 6, 8, 24, and 48 hr after excision. Each measurement was made on three shoots.

Experiment 3

Plants were grown as in Experiment 1 during July to August in a glasshouse kept at 40.9 ± 2.9 °C Tmax and 25.1 ± 1.0 °C Tmin, with SR of 10.9 ± 5.6 MJ/m²/day. Three weeks after planting, plants with 3 fully expanded leaves were water-stressed for 3 days as in Experiment 1, and then well-irrigated daily. Chlorophyll fluorescence and water potential of leaves were measured at 0, 2, 4, 6, 8, 24, 48, and 72 hr after re-irrigation. Four plants were used per measurement.

Experiment 4

Plants were grown as in Experiment 3. Five weeks after planting, whole leaves of well-irrigated plants with 4 fully expanded leaves were sprayed with about 70 ml aqueous solution of (+)-s-ABA at concentrations of 0 (control), 0.01, 0.05, 0.25, and 1.00 mM. Chlorophyll fluorescence of leaves was measured 0, 1, 3, and 6 days after

ABA application. Three plants were used for each measurement.

Measurement of chlorophyll fluorescence

Fluorescence was measured on the second expanded leaves (the third leaves were used in Experiment 3) with a fluorometer (SF-20, Richard Branker Research Ltd. Ottawa, Canada). After the fluorescence measurement, all leaves of intact plants or derooted shoots were subjected to heat stress by dipping them for 10 min in water bath held at 45 °C. Afterwards, fluorescence of the same leaf was again measured. The values of F_0 , constant yield, and F_m , maximal yield of fluorescence were provided by the fluorometer, and F_v/F_m value was obtained according to the formula of $(F_m - F_0)/F_m$. The percentage of F_v/F_m values remaining after the heat stress treatment was calculated as an indicator of thermotolerance of PA.

To determine the effect of water absorption by leaves during heat stress on chlorophyll fluorescence emission, detached leaves either sealed in thin polyvinylidene chloride film or unsealed were dipped in a water bath at 45 °C for 10 min. Unsealed leaves absorbed water and thus had higher water potential than did sealed leaves (Table 1). However, F_v/F_m values of unsealed leaves did not differ from those of sealed leaves. The results indicate that water absorption by leaves during the 10-min heat stress treatment exerted little influ-

ence on chlorophyll fluorescence. Therefore, for the convenience of operation, unsealed leaves were used for heat stress treatment in subsequent experiments.

Measurement of leaf water potential

Leaf discs of about 12 cm² area were cut with a razor blade from leaves on the same leaf position as those for chlorophyll fluorescence measurement. Water potential of leaves before heat stress treatment was measured with a thermocouple psychrometer (HR-33T, Wescor Inc., Logan USA) connected to a XY recorder (SS 100F MM, Sekonic, Tokyo Japan). Three or four leaves were used per measurement.

Results

Exp. 1. Changes in thermotolerance of PA in plants water-stressed by withholding water

Leaves wilted slightly after 1 day of withholding water but severely after 6 days. The leaves recovered turgor during the night for the first 4 days of water stress. Thermotolerance of PA in the treated leaves gradually increased within 6 days, as evidenced by higher F_v/F_m values than those of the control leaves (Fig. 1). A rapid increase in the tolerance occurred after 6 days of water stress treatment when leaf water potential fell below -1.0 MPa. The maximum thermotolerance was attained at -1.5 to -2.0 MPa, but

Table 1. Effect of sealing the detached leaves with plastic film during heat stress treatment on their water content, water potential and F_v/F_m values after heat stress treatment. Leaves were detached from plants, water-stressed by withholding irrigation, sealed or unsealed with polyvinylidene chloride film, and then dipped for 10 min in a 45°C water bath.

Days of water stress treatment	Leaves	Water content	Water potential	remaining F_v/F_m^z
0	Sealed	84.2a ^y	- 0.16a	0.071a
	Unsealed	86.2b	- 0.08b	0.060a
3	Sealed	80.7a	- 0.93	0.359a
	Unsealed	84.5b	- 0.67b	0.347a
6	Sealed	73.1a	- 1.51a	0.411a
	Unsealed	82.8b	- 0.58b	0.446a

^z F_v/F_m values of leaves water-stressed for 0, 3 and 6 days were 0.498, 0.426 and 0.487, respectively.

^y Means in columns followed by the same letter are not significantly different at $p=0.05$ by T-test.

when leaf water potential was lowered to -4.0 MPa, thermotolerance decreased (Fig. 1, inset). Thermotolerance of PA of control leaves changed slightly during experimental period.

Exp. 2. Changes in thermotolerance of PA in leaves of excised shoots with increasing loss of water

When the excised shoots were placed in an open atmosphere, the leaves lost turgor within several minutes. Thermotolerance of PA in these leaves increased rapidly corresponding to the decrease in water potential (Fig. 2). A slight rise in water potential 8 hr after shoot excision, which was probably caused by absorption of water vapor from the atmosphere after sunset, resulted in a slight reduction in thermotolerance. The relationship between the decrease in water potential and

the increase in thermotolerance was approximately linear until water potential was lowered to -0.8 MPa. When the water potential of leaves was decreased to -0.8 to -1.2 MPa, little damage to PA occurred from the 10-min heat treatment at 45°C (Fig. 2, inset).

Exp. 3. Changes in thermotolerance of PA during recovery of leaves from water stress

When plants were water-stressed for 3 days, leaves wilted moderately during the day-time, and water potential of the leaves was lowered to -1.0 MPa by the end of the water stress treatment (Fig. 3A). Leaf water potential of the water-stressed plants increased rapidly during the first 6 hr of re-irrigation, and attaining the level of the control plants after 24 hr. Leaves recovered turgor within

Fig. 1. Changes in leaf water potential (A) and thermotolerance of PA as evaluated by the percentage of Fv/Fm remaining after heat stress treatment (B) in intact water-stressed (●) and control (○) cucumber plants. The inset shows the relationship between the leaf water potential and percentages of remaining Fv/Fm. Vertical bars show the standard error of means of four replications.

Fig. 2. Changes after water stress in leaf water potential (A) and thermotolerance of PA as evaluated by the percentage of Fv/Fm remaining after heat stress treatment (B) in excised cucumber shoots. The inset shows the relationship between the leaf water potential and percentages of remaining Fv/Fm. Horizontal bars indicate the day (□) and night (■). Vertical bars show the standard error of means of three replications.

6 hr after start of re-irrigation, exhibiting no sign of wilting thereafter, even though the leaf water potential was slightly but significantly lower than that of the control plants from 24 hr onward.

Thermotolerance of PA in water-stressed leaves increased temporarily during the first 2 hr, and then decreased rapidly to the level of the control plants within 24 hr (Fig. 3B). The almost complete loss of water-stress-induced thermotolerance occurred when water potential was increased to -0.5 MPa, at which time the leaves had become fully turgid (Fig. 3, inset).

Exp. 4. Changes in thermotolerance of PA with application of exogenous ABA to leaves

Exogenous ABA applied to leaves caused an increase in thermotolerance of PA in the leaves (Fig.

4). The extent of the increase was dependent on the concentration of ABA. Leaves treated with 1.00 mM ABA showed nearly complete tolerance of PA at day 1 and maintained this high tolerance for at least 6 days. However, leaves sprayed with lower concentrations of ABA showed a decrease in tolerance of PA at day 3 after the peak tolerance was attained at day 1. Leaves treated with 0.01 to 0.05 mM ABA lost ABA-induced thermotolerance of PA almost completely at day 3.

Discussion

In the present study, heat stress damage to PA in leaves was evaluated on the basis of F_v/F_m values of chlorophyll fluorescence emission. The decrease in F_v/F_m is directly correlated with loss of PSII activity of thylakoid membranes and thus a good indicator of heat damage to PA (Berry and Björkman, 1980). The results of the present study demonstrated clearly that thermotolerance of PA in cucumber leaves was significantly enhanced in response to water stress treatment. Development of thermotolerance as well as its loss was very rapid as evidenced in that the tolerance was induced within several hours of water stress in leaves of excised shoots (Fig. 2), and the tolerance acquired during the 3-day water stress treatment was completely lost within 1 day of recovery from water stress (Fig. 3). This rapid response leads us to postulate that water stress plays a role in heat

Fig. 3. Changes during recovery from water stress in leaf water potential (A) and thermotolerance of PA as evaluated by the percentage of F_v/F_m remaining after heat stress treatment (B) in intact water-stressed (●) and control (○) cucumber plants. The inset shows the relationship between the leaf water potential and percentages of remaining F_v/F_m . Vertical bars show the standard error of means of four replications.

Fig. 4. Effects of foliar sprays of 0 (○), 0.01 (●), 0.05 (□), 0.25 (△) and 1.00 (■) mM ABA on thermotolerance of PA as evaluated by the percentage of F_v/F_m remaining after heat stress treatment. Vertical bars show the standard error of means of three replications.

acclimation in cucumber leaves, since acclimation of plants to heat stress is usually very rapid (Chen et al., 1982; Donald and Jerome, 1991).

Acquisition of thermotolerance of PA by water-stressed leaves was apparently related directly to the decrease in the leaf water potential. However, the response of leaves on water-stressed intact plants was not sensitive to a decrease in leaf water potential as compared to that on excised shoots; water potential of about -1.0 MPa resulted in only a small increase in thermotolerance of PA in the former plants, but the maximum tolerance was induced at -0.8 MPa in the latter (Compare Fig. 1 and 2, insets). Water-stressed intact plants regained turgor during the night because of reduced transpiration and increased water absorption from the soil and humid air. This may have partially canceled the heat-acclimating processes acquired by leaves during the day; thermotolerance of PA induced by water stress was lost very rapidly with re-irrigation as shown in Experiment 3 (Fig. 3).

There is a considerable amount of evidence that the level of ABA in plants increases with increasing water deficit (Hartung and Davies, 1991). The response of ABA synthesis to water status of plants is very rapid; ABA accumulates in plants within several hours of water deficit (Walton et al., 1976), but is metabolized very rapidly upon rehydration (Vernieri et al., 1994). In the present study, thermotolerance of PA in cucumber leaves changed rapidly in response to increases in water deficit and rehydration in a quite similar manner to the endogenous ABA levels as described above. In addition, exogenous ABA was effective in inducing thermotolerance in cucumber leaves and the induction of thermotolerance by ABA was dependent on its concentrations (Fig. 4). That the effect of exogenous ABA was only temporary at lower concentrations may be partly attributed to the rapid metabolism of the compound in turgid leaves (Zeevaart and Boyer, 1984). Although we obtained no direct evidence that endogenous ABA is involved in heat acclimation by water stress, the results in this study suggest that acquisition of thermotolerance of PA by water-stressed cucumber leaves was mediated through the increased levels of endogenous ABA in leaves.

Heat stress injury in leaves often accompanies desiccation stress injury because of increased loss

by transpiration (Treshow, 1970). In this case, exogenous ABA may enhance thermotolerance of leaves by causing stomatal closure and thus ameliorating water loss (Jones and Mansfield, 1970; Takahashi et al., 1993). In this study, however, leaves did not become desiccated during heat stress because the heat treatment involved dipping unsealed leaves in hot water. Consequently, the enhanced thermotolerance of PA in cucumber leaves by exogenous ABA and water stress probably resulted from their direct or indirect action to the PA. As F_v/F_m reflects the state of thylakoid membrane and its decrease has been suggested to correlate with damage or inhibition of PSII or closely to their reaction centers (Krause and Santarius, 1975; Pearcy et al., 1977). Heat stress may produce conformational changes in PSII proteins resulting in their denaturation, polypeptide chain unfolding and coagulation. Since water stress and ABA are known to induce the accumulation of heat-stable proteins called dehydrins (Close et al., 1989; Jacobsen and Shaw, 1989), it seems possible that water stress and exogenous ABA confer heat tolerance of the thylakoid membrane proteins. Further studies are needed to elucidate the physiological bases of thermotolerance induction in PA by water stress and exogenous ABA.

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水ストレスおよび外生 ABA によるキュウリ葉における光合成器官の高温耐性の変化

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摘 要

キュウリ葉の光合成器官の高温耐性に及ぼす水ストレスおよび外生 ABA の影響を調べた。水ストレス処理としては、灌水を停止して無傷苗に水ストレスを与えるか、子葉下端で切断した断根苗をガラス室で自然に脱水させるかのいずれかの方法によった。高温処理は、茎に着いたままの葉を 45℃ のウォーターバスに 10 分間浸漬して行った。水ストレスは葉の水ポテンシャルにより、また、光合成器官の高温耐性は高温処理後の葉緑素蛍光相対値 (F_v/F_m) によってそれぞれ評価した。

無傷苗では、葉の光合成器官の高温耐性は、水ポテンシャルが -1.0 MPa 以下に低下すると著しく増大し、約 $-1.5 \sim -2.0$ MPa で最大になった。断根苗でも無傷苗と同様に、光合成器官の高温耐性は水ポテンシャルの低下につれて増大し、 -0.8 MPa で最大となった。

3 日間断水により水ポテンシャルが -1.0 MPa になった無傷苗に再灌水すると、葉の水ポテンシャルは 24 時間以内に当初から -0.2 MPa を示した対照のレベルへ急激に上昇した。しかし、葉の光合成器官の高温耐性は再灌水後 2 時間のうちに一時増大し、その後対照のレベルまで急に低下した。外生 ABA は光合成器官の高温耐性を高め、濃度が高いほど効果が大きかった。 1.00 mM の ABA では、処理 1 日後に当初の 5 倍の高温耐性が得られ、この高い耐性は少なくとも 6 日間維持された。低濃度 (0.01 と 0.25 mM) の ABA では、キュウリ葉の光合成器官の高温耐性は処理 1 日後に最大値に達したが、処理 3 日後には当初のレベルまで低下した。以上の結果から、水ストレスによるキュウリ葉の光合成器官の高温耐性の増大は、葉での内生 ABA の蓄積によると考えられる。