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Damaging mechanisms of chilling- and salt stress to *Arachis hypogaea* L. leaves

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Abstract

To investigate damaging mechanisms of chilling and salt stress to peanut (*Arachis hypogaea* L.) leaves, LuHua 14 was used in the present work upon exposure to chilling temperature (4°C) accompanied by high irradiance (1,200 μmol m^{-2} s^{-1}) (CH), salt stress accompanied by high irradiance (1,200 μmol m^{-2} s^{-1}) (SH), and high-irradiance stress (1,200 μmol m^{-2} s^{-1}) at room temperature (25°C) (NH), respectively. Additionally, plants under low irradiance (100 μmol m^{-2} s^{-1}) at room temperature (25°C) were used as control plants (CK). Relative to CK and NH treatments, both the maximal photochemical efficiency of PSII (F_v/F_m) and the absorbance at 820 nm decreased greatly in peanut leaves under CH and SH stress, which indicated that severe photoinhibition occurred in peanut leaves under such conditions. Initial fluorescence (F_o), $1 - q_P$ and nonphotochemical quenching (NPQ) in peanut leaves significantly increased under CH- and SH stress. Additionally, the activity of superoxide dismutase (SOD), one of the key enzymes of water-water cycle, decreased greatly, the accumulation of malondialdehyde (MDA) and membrane permeability increased. These results suggested that damages to peanut photosystems might be related to the accumulation of reactive oxygen species (ROS) induced by excess energy, and the water-water cycle could not dissipate energy efficiently under the stress of CH and SH, which caused the accumulation of ROS greatly. CH and SH had similar damaging effects on peanut photosystems, except that CH has more severe effects. All the results showed that CH- and SH stress has similar damaging site and mechanisms in peanut leaves.

Additional key words: chilling temperature; peanut; photoinhibition; reactive oxygen species; salt stress.

Introduction

In agricultural systems, abiotic stresses, *e.g.* salinity and chilling temperature, are responsible for most of the reduction that differentiates yield potential from harvestable yield (Boyer 1982).

Chilling temperature is a kind of abiotic factors limiting the growth and distribution of plants. The membrane lipid-phase transformation is the most notably change among the changes of physiology and biochemistry

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Abbreviations: APX – ascorbate peroxidase; CH – chilling temperature accompanied by high irradiance; CK – control plants; F_m – maximum yield of fluorescence; F_m^0 – maximum yield of fluorescence measured after dark adaptation for more than 2 h at room temperature; F_m' – the maximum yield of fluorescence in light-acclimated leaves; F_o – initial fluorescence; F_o' – the initial fluorescence in light-adapted leaves; F_v – variable fluorescence; F_v/F_m – the maximal photochemical efficiency of PSII; F_s – the steady-state fluorescence yield; MDA – malondialdehyde; NH – high-irradiance stress at room temperature; NPQ – nonphotochemical quenching; OEC – oxygen-evolving complex; PFD – photon flux density; PSI – photosystem I; PSII – photosystem II; q_P – photochemical quenching; ROS – reactive oxygen species; SH – salt stress accompanied by high irradiance; SOD – superoxide dismutase; TBA – thiobarbituric acid; TCA – trichloroacetic acid.
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during plant cold acclimation. Lyons and Chapman (1976) reported that the first damage of chilling temperature to chilling-sensitive plants caused the membrane lipid-phase transition of cells, *i.e*. from liquid phase into gel phase, channels and cracks appeared on membrane, membrane permeability to ions increased and the activity of membrane-binding enzymes decreased. Chilling temperature usually affects the content of membrane lipid components and fatty acid composition, and there is a close relationship between the changes of fatty acid composition and the fluidity and stability of membrane (Allen and Ort 2001, Li *et al.* 2005). It has been reported that chilling temperature decreased CO_2 assimilation by decreasing the activity of some enzymes and caused the accumulation of excess reducing power at PSI, and PSI photoinhibition was the main factor limiting the subsequent recovery of photosynthesis after chilling stress (Li *et al.* 2004b).

Salt stress can lead to changes in development, growth, and productivity of plants, and severe stress may threaten their survival. Salt in the soil water inhibiting plant growth involves two aspects: one is the osmotic or water-deficit effect of salinity when the presence of salt in the soil solution reduces the ability of the plant to take up water, and this leads to slower growth; the other is the salt-specific or ion-excess effect of salinity when excessive amounts of salt entering the transpiration stream will eventually injure cells in the transpiring leaves and this may further reduce growth (Munns *et al.* 2006).

In the field, chilling- and salt stress very often occurs in combination with light stress, and effects of chilling temperature and salt stress on PSII under light stress have been reported in great amounts. Chilling temperature and salt stress apparently enhance the inhibition by light of plant PSII (Powles 1984, Li *et al.* 2005). At the physiological level, the multitude of effects of chilling- and salt stress indicates the importance of protecting the organism from damage by reactive oxygen species (ROS) to impair photosynthesis (Dat *et al.* 2000, Li *et al.* 2004b, 2005). It has been convinced that above 50% of ascorbate peroxidase (APX) belongs to membrane-bound enzyme, and the membrane lipid-phase transition would affect its activity to scavenge reactive oxygen species (Sonoike and Terashima 1994).

As one of the important oil crops in China, and even in the world, the high and stable yield of peanut (*Arachis hypogaea* L.) is very important to guarantee food supply. Peanut, a warm-like crop, is widely cultivated in China. However, peanut is subjected to chilling temperature sometimes in northeast region of China, which latitude is between 45–55°. Additionally, the area of the saline-alkaline land in China is very large but effects of salt stress on peanut are unclear. Many studies on cultivated physiology in the fields have been mentioned (Rao and Zhao 1989, Ketring 1979), but the damaging mechanisms of chilling- and salt stress to PSII and PSI of peanut leaves have been seldom mentioned. In the present work, the effects of chilling- and salt stress to PSII and PSI of peanut leaves were analyzed when detached peanut leaves were exposed to chilling temperature and salt stress accompanied by the high irradiance for several hours, respectively. It seemed that chilling- and salt stress had similar effects on peanut photosystems, except that more severe photoinhibition of PSII and PSI was detected under chilling stress relative to that under salt stress.

Materials and methods

Plants and stress treatments: Peanut (*Arachis hypogaea* L. Luhua 14) was used in the experiments. Seeds were first germinated wrapped in moistened filter paper at 30°C for 2 days. Sprouted burgeons were then planted into plastic pots (one plant per pot) filled with sterilised soil and grown at 25–30/15–20°C (day/night) under 13-h photoperiod (100 μmol m^{-2} s^{-1} PFD) in a greenhouse. Functional leaves from plants were used in the experiments. Leaf petioles were cut in water to get detached leaves.

To induce chilling stress (CH), with the adaxial side faced-up, the detached leaves floated on 6°C water for 6 h under 1,200 μmol m^{-2} s^{-1} PFD provided by halogen lamp.

To induce salt stress (SH), the petiole of compound leaf was dipped into water solution with 200 mM NaCl for 3 h under 20–40 μmol m^{-2} s^{-1} PFD, and then compound leaves were floated on 200 mM NaCl solution for 6 h under 1,200 μmol m^{-2} s^{-1} PFD provided by halogen lamp.

To induce high irradiance treatment (NH), with the adaxial side faced-up, the detached leaves floated on 25°C water for 6 h under 1,200 μmol m^{-2} s^{-1} PFD provided by halogen lamp.

Nonstress controls (CK) were treated at room temperature (25°C) under 100 μmol m^{-2} s^{-1} PFD.

Chlorophyll (Chl) *a* fluorescence measurements: The maximal photochemical efficiency of PSII (F_v/F_m) expressed as the ratio of variable fluorescence (F_v) to maximum yield of fluorescence (F_m) was measured with a portable fluorometer (*FMS2, Hansatech*, King's Lynn, UK) according to the protocol described by van Kooten and Snel (1990), and initial fluorescence (F_o), which was measured by an analytical light of 6 nmol m^{-2} s^{-1} PFD, was recorded after dark adaptation for more than 2 h, and subsequently a saturating pulse (6,000 μmol m^{-2} s^{-1} PFD, 0.6 s) was given to measure F_m. Nonphotochemical quenching (NPQ) and photochemical quenching (q_P) were calculated as $NPQ = F_m^0/F_m' - 1$ and $q_P = (F_m' - F_s)/(F_m - F_o')$ according to Schreiber *et al.* (1994), respectively, where F_m^0 was measured after dark

adaptation for more than 2 h at room temperature prior to stress, F_m' is the maximum yield of fluorescence in light-acclimated leaves, F_o' is the initial fluorescence in light-adapted leaves, F_s is the steady-state fluorescence yield. To induce F_s, a continuous actinic light (400 μmol m^{-2} s^{-1} PFD, 3 s) was given, and then a saturating pulse (6,000 μmol m^{-2} s^{-1} PFD, 0.6 s) was given to measure F_m'. F_o' was measured using a 3-s far red light (6 μmol m^{-2} s^{-1} PFD) when actinic light was turned off.

820 nm absorbance: The measurement of the absorbance at 820 nm was made by using a PEA (Plant Efficiency Analyser) senior (*PEA, Hansatech*, King's Lynn, UK) according to the protocol described by Schansker *et al.* (2003). The first reliable measuring point for fluorescence change was at 20 μs, whereas the first measuring point for transmission change was at 400 μs. The time constant used for the transmission measurements was 100 μs. The light intensity used for the transmission measurements was 3,000 μmol m^{-2} s^{-1} PFD. The light was produced by four 650 nm LEDs (light-emitting diodes). The far-red source was a *QDDH73520 LED* (*Quantum Devices Inc*., Barneveld, WI, USA) filtered 720 ± 5 nm. The modulated (33.3 kHz) far-red measuring light was provided by an *OD820 LED* (*Opto Diode Corp*., Newbury Park, CA, USA) filtered 830 ± 20 nm. Executing commands such as turning on and off the LEDs took approximately 250 μs. Turning on the red light and starting the measurement were synchronized commands. For the far-red light there was a delay of 250 μs between turning on the far-red light and the start of the measurement.

Superoxide dismutase (SOD) determination: 0.5 g of leaves without midrib was thoroughly ground with a cold mortar and pestle in an ice bath. The grinding medium was 4 cm^3 of 0.05 M phosphate buffer (pH 7.8), plus homogenizing glass beads. The homogenate was centrifuged at 3,000 × *g* for 15 min at 0–4°C. The supernatant, hereafter referred to as crude SOD extract, was used for determination.

SOD assay described by Giannopolitis and Ries (1977) was used with some modification. The reaction mixture was composed of 13 mM methionine, 75 μM NBT, 10 μM EDTA-Na_2, 2 μM riboflavin, and the appropriate volume of extract [in the blanks, 0.05 M phosphate buffer (pH 7.8) instead of extract]. Distilled H_2O was added to bring the final volume of 3 cm^3. The mixtures were irradiated in glass tubes selected for uniform thickness and colour. Identical solutions that were not irradiated served as blanks. The absorbance at 560 nm of the reaction mixture was determined using a UV-visible spectrophotometer (*UV-1601*, *Shimadzu*, Japan). Each treatment was repeated 5 times.

Malondialdehyde (MDA) content determination: MDA content was determined by the thiobarbituric acid (TBA) reaction according to the method of Zhao *et al.* (1994). 1.0 g roots/leaves were thoroughly ground with a cold mortar and pestle in 10 cm^3 of 10% trichloroacetic acid (TCA) reagent. The homogenate was centrifuged at 5,000 × *g* for 10 min. The supernatant, hereafter referred to as crude MDA extract, was used for determination. The reaction mixture contained 2.0 cm^3 MDA extract and 2.0 cm^3 0.6% TBA reagent [0.6% (m/v) TBA dissolved in 10% (m/v) TCA], 2.0 cm^3 distilled water instead of MDA extract was added in the blanks. After heating at 100ºC for 15 min in a water bath, the mixture was quickly cooled in an ice bath and centrifuged at 5,000 × *g* for 10 min. Absorbance was read at 450 nm, 532 nm and 600 nm. Each treatment was repeated 5 times.

Electric conductivity was measured according to revised method of Yao *et al.* (2009). 0.5 g of leaf discs with diameter of 0.8 cm were rinsed 3 times by deionized water, and then were dipped into deionized water in closed tube for 30 min vacuum pumping. The primary conductivity was measured using a *DDS-11A* (Shanghai, China) conductivity meter after 3 h oscillation, and CK conductivity was also measured. The tubes containing samples were treated with boiling water for 30 min and the final conductivity was measured when the samples were allowed to cool to room temperature. The results were expressed as: relative conductivity [%] = (primary conductivity – CK) × 100/(final conductivity – CK).

Statistical analysis: All of the measurements were performed 5 times, and the means and calculated standard deviations (SD) are reported.

Results

Photoinhibition of peanut PSII and PSI under CH and SH stress: Upon exposure to CH and SH stress, the oxidized P700 ($P700^+$) (Fig. 1*B*), which reflects photoinhibition of PSI, was calculated by the transmission at 820 nm, and photoinhibition of PSII was estimated by measuring the maximal photochemical efficiency of PSII (F_v/F_m) (Fig. 1*A*) in peatnut leaves. As shown in Fig. 1*B*, at the end of the stress, $P700^+$ decreased by 19.4%, 79.5% and 42.2% in peanut leaves under NH, CH and SH stress, respectively, relative to CK. Simultaneously, F_v/F_m in peanut leaves decreased by 33.3%, 79.5%, and 50.6% under NH, CH and SH, respectively (Fig. 1*A*).

PSII RC's activities and energy dissipation of peanut photosystems under CH and SH stress: Relative to CK, an increase of F_o was observed in NH, CH, and SH leaves during stress (Fig. 2*A*). The parameter $1–q_P$ is an estimate of the fraction of reduced primary acceptor of PSII, Q_A

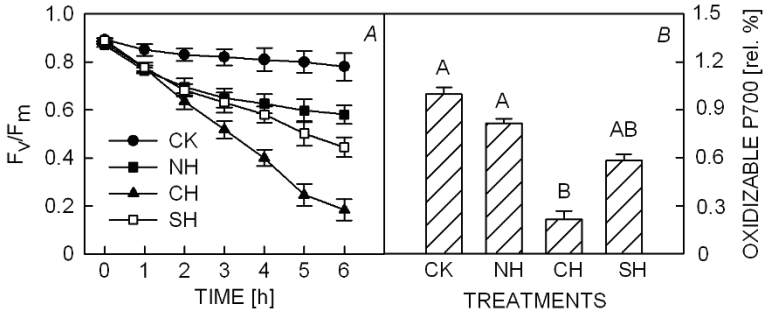

Fig. 1. Effects of CH- and SH stresses on the maximal photochemical efficiency of PSII (F_v/F_m) (*A*) and the oxidizable P700 (*B*) in peanut leaves. Each point represents the means ± SD of 5 measurements on separate leaves. The difference between CK and stresses (*i.e.* NH, CH and SH) in Fig. 1*A* is significant (P<0.05). Different letters in Fig. 1*B* indicate significant difference (P<0.05).

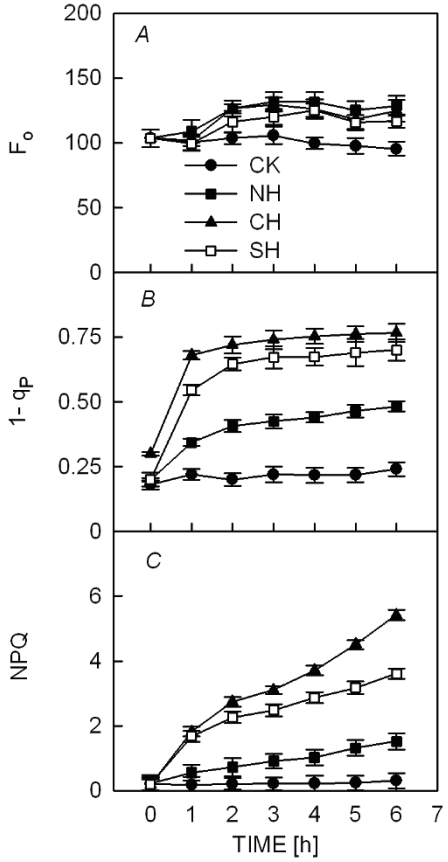

Fig. 2. Changes of minimum fluorescence (F_o) (*A*), the reduction state of Q_A ($1-q_P$) (*B*) and non-photochemical quenching (NPQ) (*C*) in different treatment peanut leaves. Each point represents the means ± SD of 5 measurements on separate leaves. The difference between control and stressed plants (*i.e.* NH, CH, and SH) is significant (P<0.05).

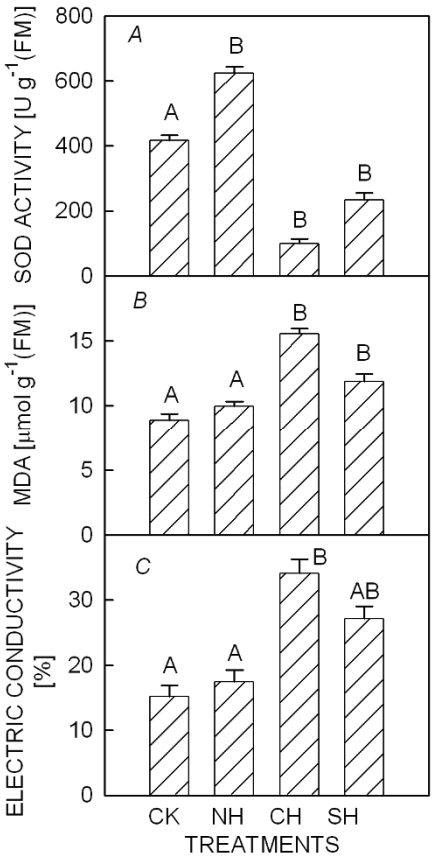

Fig. 3. Changes of SOD activity (*A*), MDA content (*B*) and electric conductivity (*C*) of peanut leaves under different treatments. Each point represents the means ± SD of 5 measurements on separate leaves. *Different letters* indicate significant difference (P<0.05).

(Havaux *et al.* 1991). Relative to CK, $1-q_P$ rose in peanut leaves under NH, CH, and SH stress, and the rate of increase was faster in peatnut leaves under stresses than in CK (Fig. 2*B*). Simultaneously, the development of NPQ grew faster in CH, SH and NH leaves relative to CK (Fig. 2*C*).

Peroxidation of membrane lipids in peanut leaves under CH and SH stress: The SOD activity of peanut leaves under CH and SH stress was significantly lower than that of CK and NH treatments (Fig. 3*A*). At the room temperature, the MDA contents of CK and NH treatment leaves were similar.

At the end of CH stress, the MDA contents of peanut leaves increased greatly compared with CK, and at the end of SH stress, the MDA contents of peanut leaves was slightly higher than that of CK and NH treatments (Fig. 3*B*).

The relative conductivity was greatly affected in peanut leaves under CH and SH stress relative to that of CK and NH treatments (Fig. 3*C*). NH stress seems not affect the membrane relative conductivity in peanut leaves relative to CK (Fig. 3*C*).

Discussion

High irradiance impairs the activity of the photosynthetic apparatus, in particular that of PSII, *via* a process known as photodamage or photoinhibition (Aro *et al.* 1993). The activities of PSII and PSI were inhibited significantly in peanut leaves upon exposure to NH, CH, and SH stress, respectively (Fig. 1), and selective photoinhibition of PSI induced by chilling temperature and low irradiance (Sonoike and Terashima 1994, Li *et al.* 2004b) and high irradiance (Li *et al.* 2007) have been a topic to be studied. It has never been reported that PSI photoinhibition could be induced by salt stress, and it seems that salt stress could aggravate photoinhibition of PSII and PSI significantly in peanut leaves under high irradiance stress (Fig. 1). PSI of peanut leaves seemed to be more sensitive to CH stress than to SH stress. This might be related to severe inhibition of photosynthesis under chilling temperature stress, which caused stromal over-reduction around PSI, and even damage to PSI (Li *et al.* 2004a, b).

The direction of F_o changes depend on the dominant factor between the energy dissipation and the inactivation or damage of PSII. An increase in NPQ leads to a decrease in F_o (Ögren and Öquist 1984) and the inactivation or the damage of PSII causes the increase of F_o (Xu and Wu 1996). Our results showed that NH, CH, and SH stress induced inactivation or damage of PSII (Fig. 2*A*). It seemed that PSII reaction centers were sensitive to environmental stress induced by high light, and chilling temperature and salt stress might aggravate the inhibition of high light to PSII reaction centers of peanut leaves (Fig. 1*A,B*). Additionally, it has been reported that D1 protein is subjected to both chilling- and salt stress accompanied by high irradiance (Murata *et al.* 1992, Vonshak *et al.* 1996, Lindahl *et al.* 2000, Allen and Ort 2001, Sudhir and Murthy 2004). Salt stress enhanced photoinhibition by inhibiting repair of PSII, *i.e.* inhibiting degradation of D1 protein in photodamaged PSII and *de novo* synthesis of D1 (Ohnishi and Murata 2006). The damage of D1 protein would block the electron transport and induce further photoinactivation of PSII reaction centers (Allen and Ort 2001). As to PSI photoinhibition of peanut leaves under SH stress, there has no evidence to show that salt stress could affect reaction center components of PSI like its action on D1 protein, and the mechanisms of PSI photoinhibition induced by salt stress needs further study.

It has been demonstrated that the extent of PSII photoinhibition is closely correlated with the redox state of Q_A under a range of stress condition (Li *et al.* 2004a, Havaux *et al.* 1991). The relative redox state of Q_A *in vivo* can be estimated as $1–q_P$. Higher $1–q_P$ in peanut leaves under NH, CH, and SH stress relative to CK (Fig. 2*B*) suggested that the extent of Q_A reduction was more severe in peanut leaves under stresses. The xanthophyll cycle-dependent NPQ mechanism constitutes an important protective response to prevent over-reduction of Q_A (Demmig-Adams and Adams 1996), and the increases in $1–q_P$ (Fig. 2*B*) were accompanied by marked increase in NPQ (Fig. 2*C*). This implies that the extent of PSII photoinhibition is closely correlated with the redox state of Q_A (Xu *et al.* 1999) in peanut leaves under CH and SH stress and the turnover rates of dark reactions are restricted, which results in the accumulation of assimilation power and protons in the thylakoid lumen.

If excess energy could not be dissipated and CO_2 assimilation was blocked under chilling temperature stress, PSI reaction centers were completely reduced to produce triplet P700, which could easily react with O_2 to generate ROS, superoxide anion, and singlet oxygen (Allen and Ort 2001, Asada 1999). Superoxide anion was mainly generated by Mehler reaction, and singlet oxygen was generated by reaction of O_2 with triplet chlorophyll or triplet $P680^+$ (Asada 1999). When exposed to CH and SH stress, the activity of SOD decreased greatly (Fig. 3*A*), SOD is one of the key enzymes to scavenge ROS produced in active cells. Peroxidation of unsaturated lipids has been mentioned as a possible cause of increased membrane rigidity in tropical and subtropical plants exposed to chilling temperature stress (Lee *et al.* 2004). In general, the increased accumulation of lipid peroxidation is indicative of enhanced production of toxic oxygen species (Dhindsa *et al.* 2001), which could be estimated by the production of MDA. It seemed that the degree of lipid peroxidation in peanut leaves increased more pronouncedly than that of CK and NH treatment under CH and SH stress (Fig. 3*B*). The degree of injury induced by CH and SH stress to issues was similar to that of lipid peroxidation in peanut leaves (Fig. 3*C*). The higher lipid peroxidation and the electric conductivity under CH and SH stress might be related to ROS accumulation induced by low SOD activity (Fig. 3*A*) and severe photoinhibition of PSII and PSI (Fig. 1).

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