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CHLOROPHYLL FLUORESCENCE AND GAS EXCHANGE RESPONSES OF MAIZE SEEDLINGS TO SALINE-ALKALINE STRESS

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Abstract

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Responses of photosynthesis rate, stomatal conductance, chlorophyll fluorescence characteristics and chlorophyll content of maize (*Zea mays* L.) seedlings under combined salinity-alkalinity stress were examined. Investigation revealed that the net photosynthesis rate (P_n) and stomatal conductance (g_s) decreased rapidly with increasing of salinity-alkalinity stress. The intercellular CO_2 concentration (C_i) decreased at low salinity-alkalinity and increased at high salinity-alkalinity. The maximal efficiency of photosystem II (PSII) photochemistry (F_V/F_M) decreased only at high salinity-alkalinity. The comprehensive photosynthesis performance index (PI_{ABS}) gradually decreased with increasing of salinity-alkalinity concentration. The JIP test showed that the electric transfer of donor side and acceptor side of PSII in maize seedlings were inhibited by high salinity-alkalinity stress. Stomatal limitation is the main reason of decreased photosynthesis rate at low salinity-alkalinity, and non-stomatal limitation, i.e. decreased photosynthesis activity in PSII plays an important role in decreased photosynthesis rate at high salinity-alkalinity.

Key words: fast chlorophyll fluorescence induction, photosystem II, photosynthesis rate, salinity-alkalinity, *Zea mays* L.

Introduction

Soil salinization is one of the reasons for crop yield reduction in arid and semi-arid areas (Khan et al., 2001). The saline and sodic soils cover about 10% of total arable lands world-widely. About 23% ($0.34x10^9$ ha) of the cultivated lands are saline and 37% ($0.56 x 10^9$ ha) are sodic (Tanji, 1990). Salinity induces many adverse effects on the photosynthesis of plants including reducing CO_2 assimilation and stomatal conductance (Bongi and Loreto, 1989; Flanagan and Jefferies, 1989) and decelerating the activity of electron transport of photosystem II (PSII) (Everard et al., 1994; Lu and Vonshak, 2002). The reduction of photosynthesis may be the consequences of stomatal closure (Downton et al., 1985; Youssef, 2007) and/or non-stomatal inhibition of photosynthesis (Jeranyama and DeMoranville, 2008). Alkalinity, al-

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though not investigated as thoroughly as salinity (Shi and Wang, 2005), inhibits photosynthesis and retards the growth of plant in some investigations (Yang et al., 2009).

Soil salinization and alkalization frequently co-occur in many areas, especially in northeastern China (Kawanabe and Zhu, 1991). To our best knowledge, only a few reports are available indicating the effect of combined salinity-alkalinity stress on plants (Anjum et al., 2005; Shi and Wang, 2005; Zhang and Yin, 2009). Previous limited studies showed that salt-alkaline mixed stress led a decrease in chlorophyll concentration (Kaya et al., 2002), stomatal conductance and transpiration rate (Khan and Abdullah, 2003), and inhibited the growth of plant. When different concentrations of salinity and alkalinity were combined, the effect on photosynthesis of plants was much more complex, but the underlying basis in photosynthetic capacity under salinity-alkalinity stress is yet not fully understood. Measurement of chlorophyll fluorescence is a potential indicator of photosynthetic efficiency in plants and be proved as a rapid, non-invasive, and reliable method to assess photosynthetic performance under environmental stress (Krause and Weis, 1991; Schreiber et al., 1994) and allows the location of primary site of damage induced by environment stress.

Maize is one of the most cultivated and widely grown crops all over the world. Unfortunately, in many areas, especially in northeastern China, the productivity of maize is significantly reduced due to soil salinization and alkalinity. The improvement of productivity of maize requires fully understanding the combined effect of salinity and alkalinity on the photosynthesis of this crop. The present study aimed at investigating the photosynthetic responses of maize under salinity-alkalinity stresses probed by chlorophyll (Chl) fluorescence and gas exchange *in vivo*.

Materials and Methods

Materials and treatments

The fully-nourished seeds of maize (*Zea mays* L).were selected sterilized by 0.1% $HgCl_2$ for 10 min and repeatedly washed by distilled water. After 12-h soaking, the seeds were cultured in an incubator for germination with a constant temperature of 28^0C. When the buds length reached 1-2 cm, the seeds were planted into sand pots under a photosynthetic photo flux density of approximately 350μmol/m^2/s, 65±5% relative humidity, a photoperiod of 14h, and a day/night temperature of $25/18^0$C. Each pot contained five seedlings. Seedlings were watered with half-strength Hoagland nutrient solution (Hoagland and Arnon, 1950) until the heights of seedlings reached around 20 cm for treatment.

Neutral salt (NaCl) and alkaline salt ($NaHCO_3$) were choused based on the main salt component in saline-alkaline soil in western Jilin Province, China. The salts were mixed in various concentrations with gradually increased salinity-alkalinity concentration as shown in Table 1. The combination of five concentrations of NaCl (12.5, 25, 50, 75 and 100 mmol/l) and $NaHCO_3$ (2.5, 12.5, 25, 50 and 100 mmol/l) were referred to SA1-SA5. Plants in salinity-alkalinity treatments were watered with half-strength Hoagland solution containing various concentration salts. Plants in control were watered with half-strength Hoagland nutrient solution without NaCl and $NaHCO_3$.

Growth measurement

Seedling heights were measured as the distance between the stem base and the shoot tip, and recorded at the beginning and the end of the experiment. The calculation of plant growth increments were estimated as follows: Height increment $=H_2-H_1$. H_1= plant height

Table 1

The concentrations of NaCl and $NaHCO_3$ in different treatments

Treatment group	NaCl, mmol/l	$NaHCO_3$, mmol/l
Control	0	0
Salinity-alkalinity 1 (SA1)	12.5	2.5
Salinity-alkalinity 2 (SA2)	25	12.5
Salinity-alkalinity 3 (SA3)	50	25
Salinity-alkalinity 4 (SA4)	75	50
Salinity-alkalinity 5 (SA5)	100	100

at start of treatment; H_2 = plant height at end of treatment.

At the end of the experiment, plants were carefully removed from the pots, and roots were thoroughly rinsed with tap water to remove the attached soil. The fresh weights of the plants were recorded.

Measurement of polyphasic fast fluorescence induction

The polyphasic fast fluorescence induction curve provides valuable information about the function of PSII (Strasser et al., 1995; van Heerden et al., 2003). Upon the triggering of strong actinic light, the increase in Chl *a* fluorescence of dark-adapted photosynthetic materials will follow a triphasic kinetic from its initial level (F_O), two intermediate level (F_J and F_I) and its maximal level (F_M or F_P) (Lazar, 2006). The initial Chl fluorescence F_O (fluorescence intensity at 50 μs) indicates all molecules of Q_A are in the oxidized state. F_J (fluorescence intensity at around 2 ms) reflects the accumulation of Q_A^-. F_I (fluorescence intensity at around 30 ms) demonstrates an accumulation of $Q_A^-Q_B^-$, whereas F_M (maximal fluorescence intensity, usually reached at 200-500 ms) indicates all molecules of Q_A are in the reduced state with the accumulation of $Q_A^-Q_B^{2-}$ (Strasser and Govindjee, 1992; Strasser et al., 1995). It can be used to analyze changes in electron transfer reaction on both donor (Delosme and Joliot, 2002) and acceptor side of PSII (Strasser and Govindjee, 1992).

The JIP-test (Strasser and Strasser, 1995) was employed to analyze each of Chl *a* fluorescence transient. F_O, $F_{300\mu s}$, F_J and F_M from the original measurements were used. The JIP-test represents translation of the original data to biophysical parameters that quantify the energy flow through PSII. The formulae (Table 2) illustrate how each of the biophysical parameters can be calculated from the original fluorescence measurements (Strasser et al., 2000).

The third full-expanded leaf was used for fast chlo-

Table 2

Formulae and terms used in the JIP-test (Strasser et al., 2000)

Formulae and terms	Illustrations
$V_J = (F_{2ms}-F_O)/(F_M-F_O)$	Relative variable fluorescence intensity at the J-step
$F_V = F_M-F_O$	Variable fluorescence
$M_O = 4(F_{300\ \mu s}-F_O)/(F_M-F_O)$	Approximated initial slope of the fluorescence transient
Quantum efficiencies or flux ratios	
$\varphi_{Po} = TR_O/ABS = [1-(F_O/F_M)] = F_V/F_M$	Maximum quantum yield for primary photochemistry (at $t = 0$)
$\varphi_{Eo} = ET_O/ABS = [1-(F_O/F_M)]\Psi_O$	Quantum yield for electron transport (at $t = 0$)
$\varphi_{Do} = 1-\varphi_{Po} = F_O/F_M$	Quantum yield for energy dissipation (at $t = 0$)
$\Psi_O = ET_O/TR_O = (1-V_J)$	Probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A (at $t = 0$)
Specific fluxes or specific activities	
$ABS/RC = M_O(1/V_J)(1/\varphi_{Po})$	Absorption flux per reaction center
$TR_O/RC = M_O(1/V_J)$	Trapped energy flux per reaction center (at $t = 0$)
$ET_O/RC = M_O(1/V_J)\Psi_O$	Electron transport flux per reaction center (at $t = 0$)
$DI_O/RC = (ABS/RC)-(TR_O/RC)$	Dissipated energy flux per reaction center (at $t = 0$)
Performance indexes	
$PI_{ABS}=(RC/ABS)[\varphi_{Po}\ (1-\varphi_{Po})][\Psi_O/(1-\Psi_O)]$	Performance index on absorption basis

rophyll fluorescence measurements with a portable fluorometer (FP100, PSI, Brno, Czech Republic). The plant leaf was dark-adapted for 10 min before fluorescence measurement. Fluorescence was excited by a visible light band peaking at 475 nm (half bandwidth 25 nm). Fast fluorescence transients induced by actinic light were recorded at sampling intervals varying from 10 μs to 10 ms.

Gas exchange measurement

After chlorophyll fluorescence measurement, the same leaves were used for measurement of net photosynthesis (P_n), stomatal conductance (g_s) and internal CO_2 concentration (C_i) at a PPFD level of 1500 μmol/m^2/s^1 at ambient CO_2 concentration (350 μmol/mol) with a portable photosynthesis system (LI-6400, LI-COR Biosciences Inc., Lincoln, USA).

Leaf chlorophyll content

Finally, the chlorophyll content of the same leave used for chlorophyll fluorescence and gas exchange measurement was measured with a CCM-200 chlorophyll content meter (Opti-Sciences, Tyngsboro, MA, USA).

Results and Discussion

Growth measurement

After 7 days, a notable reduction (64% and 93%, at SA3 and SA5 treatment) in height increment of maize seedling was observed (Figure 1). Height increments of treated plants decreased gradually with increasing salinity-alkalinity concentration. The fresh weight per plant was also affected by salinity-alkalinity stress. The fresh weights of plants under SA3, SA4 and SA5 treatment were only 83%, 61% and 53% of control, respectively (Figure 2). The plant growth and fresh weight were markedly reduced with increasing salinity-alkalinity concentration, which is in good agreement with pervious studies. Shoot growth in maize seedling appears to be sensitive to salinity stress (Bilgin et al., 2008). Restriction in plant height and aboveground biomass is one of the obvious symptoms of salinity-alkalinity stress (Guan et al., 2009; Yang et al., 2008), which mainly resulted from the inhibited expansion of new leaves and the elongation of shoot. The restriction in leaf expansion under saline-alkaline conditions minimizes water losses, which happens to many species under osmotic stress (Ribeiro et al., 2006; Tabatabaei, 2006).

Photosynthesis analysis

The responses of net photosynthesis rate (P_n), stomotal conductance (g_s) and intercellular CO_2 concentration (C_i) under different salinity-alkalinity treatments were shown in Table 3. There was a clear decreasing tendency for photosynthesis rate and stomatal conductance. As shown in Table 3, the P_n was down-

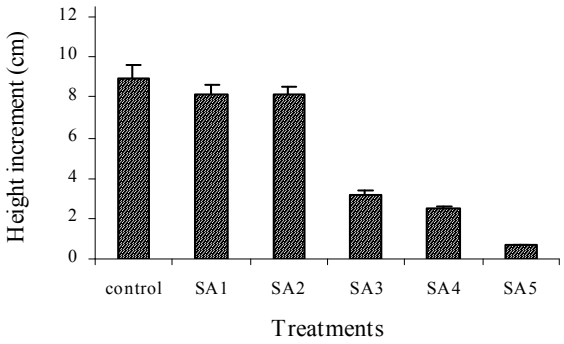

Fig.1. Height increments of maize seedlings exposed or not (control) to salinity-alkalinity stresses (SA1-SA5). Data points and error bars represent mean ± S.E. of five replicates (n = 5).

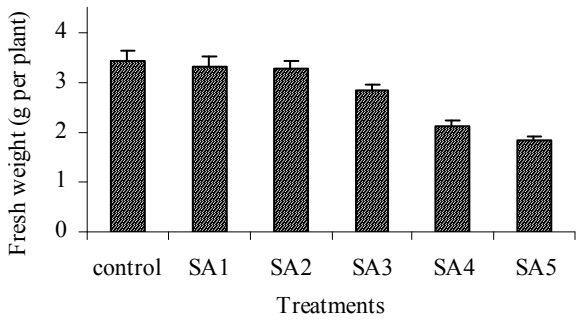

Fig. 2. Fresh weights of maize seedling under salinity-alkalinity (SA1-SA5) stresses and control condition. Data points and error bars represent mean ±S.E. of five replicates (n = 5)

Table 3

Effect of salinity-alkalinity (SA1-SA5) stresses on the leaf net photosynthesis (P_n), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i)

Treatment group	P_n (μmol CO_2 /m^2/s)	g_s (mol H_2O /m^2/s)	C_i (μmol/mol)
Control	20.80 ± 1.51	0.158 ± 0.011	116 ± 12
SA1	20.77 ± 1.00	0.146 ± 0.009	102 ± 9
SA2	15.97 ± 1.26	0.103 ± 0.007	86 ± 10
SA3	12.37 ± 0.78	0.080 ± 0.006	89 ± 5
SA4	1.09 ± 0.02	0.036 ± 0.001	296 ± 6
SA5	-3.61 ± 0.05	0.026 ± 0.002	597 ± 6

regulated to 60% and 0% of control at SA3 and SA5 treatment, respectively. The sensitivity of P_n is an ideal indicator under saline stress (Rozema and van Diggelen, 1991), as well as under salinity-alkalinity stress in present study. This was in agreement with many studies (Xu et al., 2008). Reduction in net photosynthesis rate was strongly correlated with depressed growth. This implies that inhibition of plant growth can be partially attributed to the reduction of carbon assimilation under stress (Lovelock and Ball, 2002). The stomotal conductance (g_s) showed a reduction from 0.158 mol H_2O /m^2/s for control to 0.08 and 0.026 mol H_2O /m^2/s for plants under SA3 and SA5 stresses. Intercellular CO_2 concentration (C_i) showed a decrease under SA1, SA2 and SA3 treatment, but a strong increase under SA4 and SA5 treatment. According to Farquhar et al. (1989), lower P_n accompanied by lower g_s (stomatal conductance) and lower C_i (intercellular CO_2 concentration) at low salinity-alkalinity (SA1, SA2 and SA3) might be mainly ascribed to stomatal closure, which restricts CO_2 entry into leaves. Whereas, lower P_n accompanied by lower g_s and higher C_i at high salinity-alkalinity (SA4 and SA5) may be attributed to non-stomatal limitation, including changes in leaf biochemistry that results in inhibition or down-regulation of photosynthesis. Past studies demonstrated that stomatal limitation is more significant at medium salinities and non-stomatal restriction is more pronounced at high salinity (Everard et al., 1994; Netondo et al., 2004), and a similar pattern under different concentration of salinity-alkalinity stress was found in present study. Present results suggest that the stomatal closure is likely the first defense of plant against salinity-alkalinity stress. Non-stomatal limitation increases progressively with the increase of salinity-alkalinity, even playing a major role, for example, through inhibiting biochemical metabolism and adversely affecting chlorophyll *a* fluorescence.

Chlorophyll fluorescence

To investigate the effect of salinity-alkalinity on the electron transport in PSII, the polyphasic fast fluorescence induction was performed. Figure 3 showed the fast kinetic induction curves of plants treated with salinity-alkalinity at different concentrations. There was no significant change of F_O under different stresses. F_M decreased drastically and the J-P phase gradually leveled off with increasing salinity-alkalinity concentration, indicating that salinity-alkalinity had inhibitory effect on the photochemical activity of maize seedling, and it is usually be explained as an increase of number of the closed PSII reaction centers, which do not participate in electron transport (Toth et al., 2005). It was observed that the peak at P step (F_M) disappeared and the J-P almost became a straight line for plants treated with SA5 stress, suggesting that electron transport chain was broken after Q_A (Haldimann et al., 1995 ; (Strasser et al., 1995; Toth et al., 2005) , and OEC failed to provide electrons for PSII to reduce the quinone acceptors (Falk and Palmqvist,

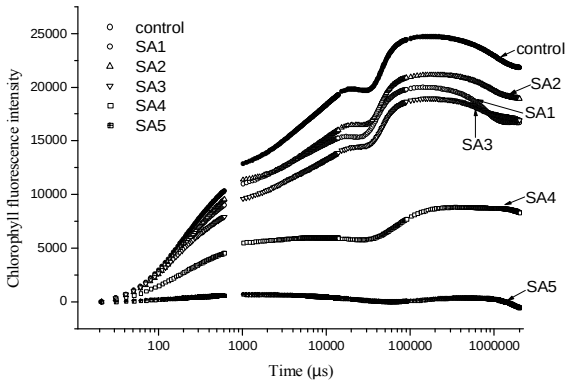

Fig. 3. Examples of fast chlorophyll fluorescence transient of maize seedlings under different salinity-alkalinity (SA1-SA5) stresses

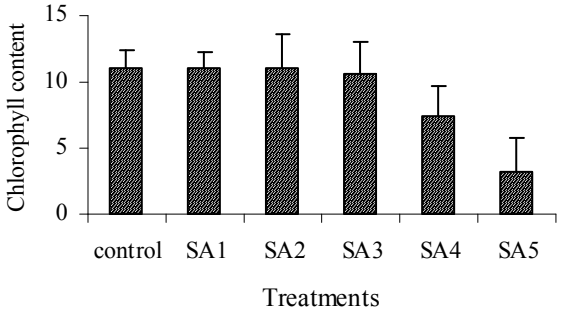

Fig. 4. Chlorophyll content of maize seedlings exposed or not to salinity-alkalinity (SA1-SA5) stresses. Data points and error bars represent mean ±S.E. of five replicates (n = 5)

1992); that is, the electron transport at the donor side of PSII was inhibited, and $P680^+$, a strong fluorescence quencher, accumulated (Govindje, 1995) at higher level salinity-alkalinity concentration. The disappearance of F_M after treated with high salinity-alkalinity indicates a complete malfunction of PSII (Schreiber et al., 1971). This result indicates that salinity-alkalinity stress had inhibitory effects on the donor side of PSII. The depression of F_M under stress condition was also found in other reports (Appenroth et al., 2001; Pan et al., 2008).

Since the O-J-I-P fluorescence transient reflects the state of Q_A, Q_B and PQ pool (Strasser and Govindjee, 1992), more information was obtained from the O-J-I-P curves according to JIP-test analysis. The selected JIP-test parameters were listed in Table 4. The decrease of F_M led to a decrease of the variable fluorescence (F_V), and finally led to a decline of maximal efficiency of PSII photochemistry (F_V/F_M). F_V decreased to 83%, 80% and 2% of control under SA1, SA3 and SA5 treatment, respectively. F_V/F_M remained relatively constant at low and moderate salinity - alkalinity, and decreased only when salinity-alkalinity concentration was high enough (83% and 6% under SA4 and SA5, respectively; Table 4). Present results were in conformity with many investigations (Larcher et al., 1990; Netondo et al., 2004; Xu et al., 2008). F_V/F_M of plants under moderate stress usually changes little, and the decline in F_V/F_M ratio under severer stress reflects a reduction in the ability of PSII to reduce the primary acceptor Q_A (Calatayud and Barreno, 2001).

It was observed that an increase of salinity-alkalinity concentration resulted in an increase of the effective antenna size per reaction center (ABS/RC, Table 4). The value of ABS/RC increased to 117% and 3400% of control under SA3 and SA5 treatment, respectively. However, the electron transport (ET_O/RC) was not significantly affected under SA1, SA2 and SA3 stresses. The values of φ_{Do} under SA3 and SA5 stresses increased to 119% and 365% of control, respectively. Similar results was reported (Zribi et al, 2009), which the electron transfer was less inhibited than photosynthesis rate/stomatal conductance at moderate stress. Lower φ_{Eo} (1% of control) and ψ_o (43% of control) under SA5 stress revealed that the activity of electron transport beyond Q_A, i.e. the acceptor side of PSII was considerably hindered at high salinity-alkalinity concentration. These changes resulted in decreases in the performance index (PI_{ABS}). PI_{ABS} decreased to 67% and 0% of control under SA3 and SA5 stresses, respectively. These changes are similar to various reports (Dernetriou et al., 2007). These parameters such as PI_{ABS}, φ_{Do} and ABS/RC, derived from JIP test, showed a greater sensitivity than F_V/F_M, being in agreement with many findings (van Heerden et al., 2003; Christen et al., 2007). This is because these parameters give infor-

Table 4

The selected parameters obtained from JIP test of the control and salinity-alkalinity treated samples. All parameters were normalized to the values of control

Treatment	F_V	F_V/F_M	Ψ_O	φ_{Eo}	φ_{Do}	PI_{ABS}	ABS/RC	TR_O/RC	ET_O/RC	DI_O/RC
Control	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%
SA1	83%	98%	102%	99%	107%	88%	106%	103%	104%	113%
SA2	82%	97%	102%	98%	109%	87%	107%	103%	105%	117%
SA3	80%	93%	98%	92%	119%	67%	117%	109%	106%	139%
SA4	63%	83%	95%	79%	148%	51%	132%	105%	99%	207%
SA5	2%	6%	43%	1%	365%	0%	3400%	111%	42%	250%

mation on the heterogeneity of PSII reactive centers, while F_V/F_M just reflects the efficiency of all the PSII units including both activated reactive centers and inactivated reactive centers (Wen et al., 2005). Present results in chlorophyll fluorescence confirmed that photosynthetic activity was more inhibited under high salinity-alkalinity than that under low and moderate salinity-alkalinity.

Chlorophyll content

To further understand the damage of salinity-alkalinity on photosynthesis, chlorophyll content was measured. After 7-days treatment, the chlorophyll contents of maize seedlings under SA1-SA3 stress were little affected, however, the chlorophyll contents of maize seedlings decreased significantly under SA4 and SA5 treatments, being 67% and 29% of the control, respectively (Figure 4). Chlorophyll content under salinity-alkalinity stress was less reduced than plant growth, except at a high level of salinity-alkalinity concentration. A decrease in leaf chlorophyll content has been described in maize irrigated with water containing high concentration NaCl (Demir and Kocacaliskan, 2008). This decrease may be attributed to the formation of proteolytic enzymes such as chlorophyllase, which is responsible for the chlorophyll degradation (Sabater and Rodriguez, 1978) as well as damaging the photosynthetic apparatus (Yasseen, 1983).

Conclusions

Chlorophyll fluorescence and gas exchange measurement provide useful tools to estimate the potential degree of injury of plant in saline-alkaline soil and determine the underlying mechanism of injury. In conclusion, the growth of maize was affected by salinity-alkalinity stress including down-regulation of plant growth and chlorophyll content, and inhibition in photosynthesis. Decreased photosynthesis rate under low salinity-alkalinity condition is associated with the increase of stomatal closure, while decreased photosynthesis rate under high salinity-alkalinity stress is mainly attributed to non-stomatal limitation, i.e. down-regulation of photochemical activity and damage of photosynthetic apparatus. Both donor and acceptor sides of PSII are the target sites under high level of salinity-alkalinity. With the increasing of salinity-alkalinity concentration, the electric transfer was gradually inhibited, and energy dissipation enhanced and finally the comprehensive photosynthesis performance index and photosynthesis rate decreased.

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