ACADEMIC JOURNALS
expand your knowledge

International Journal of Plant Physiology and Biochemistry

Full Length Research Paper

Effects of salinity stress on growth in relation to gas exchanges parameters and water status in amaranth (*Amaranthus cruentus*)

Christophe Bernard Gandonou[1*], Hermann Prodjinoto[1,2], Séraphin Ahissou Zanklan[1], Agapit Dossou Wouyou[1], Stanley Lutts[2], David Hambada Montcho[3], Françoise Assogba Komlan[4] and Armel Clément Goudjo Mensah[4]

[1]Unité de Recherche sur l'Adaptation des Plantes aux Stress Abiotiques, les Métabolites Secondaires et l'Amélioration des Productions Végétales, Laboratoire de Physiologie Végétale et d'Etude des Stress Environnementaux, Faculté des Sciences et Techniques (FAST/UAC), 01BP526, Tri Postal, Cotonou, République du Bénin.
[2]Groupe de Recherche en Physiologie Végétale, ELI-A, Bâtiment Croix du Sud, Université Catholique de Louvain, Louvain-La-Neuve, Belgique.
[3]Ecole de Gestion de la Production Végétale et Semencière, Université Nationale d'Agriculture, Kétou, République du Bénin.
[4]Centre de Recherches Agricoles sur les Plantes Pérennes, Institut National des Recherches Agricoles du Bénin, INRAB, Abomey-Calavi, Bénin.

Salinity is a major detrimental abiotic factor for plant growth. The main purpose of this study was to analyze the effects of different NaCl concentrations on growth and some physiological parameters related to gas exchanges and water relations in amaranth (*Amaranthus cruentus*) plants. Three weeks old amaranth plants from the cultivar 'Locale' were exposed in nutrient solution to 0, 30 or 90 mM NaCl (electrical conductivities of 1.915; 4.815 and 11.70 dS.m^{-1} respectively) in phytotron conditions. Shoot elongation as well as fresh and dry masses of shoot and root were determined after two weeks of stress exposure. Net photosynthesis (A), intercellular CO_2 concentration (Ci), instantaneous transpiration (E), stomatal conductance (gs), osmotic potential (Ψs) as well as the efficiency of the instantaneous carboxylation (A/Ci), intrinsic (A/gs) and instantaneous (A/E) water use efficiency were estimated. Results reveal that salt stress induced a significant reduction in growth of aerial part as well as net photosynthesis, instantaneous transpiration, stomatal conductance and leaf and root osmotic potentials. In contrast, no significant reductions were recorded for root growth, shoot water content, intercellular CO_2 concentration and instantaneous carboxylation efficiency. However, a significant increase was observed for intrinsic (A/gs) and instantaneous (A/E) water use efficiency. The plant growth reduction observed hinges upon a drop in photosynthetic activity due mainly to stomatal closure. These data suggest that photosynthetic activity may be used as a reliable criterion for physiological estimation of salt-tolerance in *A. cruentus* cultivars.

Key words: Saline stress, net photosynthesis, stomatal conductance, osmotic potential, water use efficiency.

INTRODUCTION

Salinity is one of the most important environmental constraints that limits plant productivity, particularly in arid and semi-arid climates (Ashraf and Harris, 2004; Hussain et al., 2009). Indeed, more than 800 million hectares of arable lands are affected by soil salinity worldwide including about 45 million hectares of irrigated lands (Munns and Tester, 2008). The problem increases due to inadequate agricultural practices (Shannon and Grieve, 1999; Villa-Castorena et al., 2003; Munns, 2005) and sea level rise (Munns, 2005). Excess of saline ions in soils generates an elevated osmotic pressure and an accumulation of toxic ions in plant tissues, notably Na^+, and consequently induces a decrease in growth and crop yield due to a disruption of several physiological processes (Munns, 2002).

Photosynthesis is an important metabolic pathway that is considered to be salt-sensitive (Munns et al., 2006; Chaves et al., 2009). Salinity reduces photosynthesis by inducing stomatal closure preventing CO_2 diffusion (Brugnoli and Lauteri, 1991). Salinity may also affect non-stomatal properties such as chlorophyll synthesis, photosystem structure, electron transport (Lee et al., 2004), efficiency of the ribulose-1,5-bisphosphate carboxylase/oxygenase for carbon fixation (Delfine et al., 1998; Jaleel et al., 2007; Megdiche et al., 2008), and photophosphorylation (Stoeva and Kaymakanova, 2008). Salt stress also impacts the water supply of the plant. Plant-water relations have rather important implications on the physiological and metabolic processes conditioning plant growth (Passioura, 2010). Salinity indeed frequently induces plant dehydration in relation to a decrease in the osmotic potential of external soil solution which prevents water absorption by the root system (Álvarez et al., 2012).

Amaranth (*Amaranthus* spp.) species are tropical crops used as pseudo-cereals or leafy vegetables with a high nutritional value and large adaptability to various environments mainly marginal lands and semi-arid regions where salinity issue is sharp (Cunningham et al., 1992; Allemann et al., 1996; Bhattacharjee, 2008). In Benin, amaranth species are extensively cultivated on the arable lands from costal zones where availability of good-quality water and salinity pose serious threats (Wouyou et al., 2016; 2017). Previous studies showed that NaCl concentrations ranging from 30 to 200 mM reduce aerial and root parts growth in different genotypes of amaranth including cultivars of *Amaranthus cruentus* (Makus, 2003; Omami and Hammes, 2005; Ornami and Hammes, 2006; Qin et al., 2013; Amukali et al., 2015; Lavini et al., 2016;

Wouyou et al., 2017). However, the physiological and biochemical mechanisms involved in such a growth reduction remain largely unknown. The main goal of the present study is therefore to analyze the effect of salinity on growth, stomatal conductance, net photosynthesis, transpiration, osmotic potential, efficiency of instantaneous carboxylation and water use efficiency in the *A. cruentus* in order to obtain additional information on the main factors limiting plant growth in this species.

MATERIALS AND METHODS

Plant material and salinity stress treatment

Seeds of the cultivar '*Locale*' were germinated in jars filled with substrate (Substrate NFU 44-551) for a week. The composition of the substrate is shown in Table 1. The obtained young seedlings were individually transferred in pots containing the same substrate for one further week in a growth chamber characterized by a 25/21°C (day/night) temperature, a 16/8 h (day/night) photoperiod, a light intensity between 150-220 $\mu mole.m^{-2}s^{-1}$ using white fluorescent tubes (F36W/840-T8). Daytime humidity was set to *c.a.* 65%. Plants were then transferred to tanks containing a modified Hoagland solution (Went, 1957) with pH 6. Stress application was carried out after one week on three weeks old plants. Treatments consisted of three NaCl concentrations: 0, 30 and 90 mM corresponding to an electrical conductivity of 1.915, 4.815 and 11.70 $dS.m^{-1}$, respectively. All treatments were repeated three times in a complete randomized design and each repetition consisted in a pooled sample of six plants. Eighteen plants were thus considered per treatment (Figure 1). Salinity stress was maintained over a period of two weeks.

Measurement of growth parameters and water contents

Shoot height, root length as well as fresh and dry biomasses of the shoot and roots were determined after two weeks of stress application. Shoot height was measured at the time of stress imposition (Hi) and after two weeks of treatment (Hf). The relative growth in height was calculated according to the formula: RHG = (Hf - Hi)/Hi. Root elongation was estimated according to the same procedure. Shoot and root fresh biomasses were determined after two weeks. Samples were then transferred to an oven at 80°C for 72 h for dry biomass determination. Water content was determined as [fresh mass - dry mass)/ fresh mass] x 100.

Measurement of physiological parameters

All physiological parameters were determined after two weeks treatment. Stomatal conductance (g_s) was estimated at the mid photoperiod on the youngest fully unfolded leaf on three plants per treatment using a porometer (AP4-UM-3, Delta-T Devices, Cambridge, United Kingdom). Net photosynthesis (*A*, net rate of

*Corresponding author. E-mail: ganchrist@hotmail.com. Tel: (00229) 97 39 69 78.

Table 1. Composition of the Substrate NFU 44-551 used for plant growth.

Component	Fertilizer	Dry matters/ raw product	Organic matters/ Dry product	pH (H2O)	Conductivity	Water retention capacity
Values	1 kg/m^3 NPK 14-8-14	50%	85%	6.5	40 mS/m	750 ml/L

Figure 1. Experimental design with plants at the beginning of stress imposition.

carbon assimilation) was measured under a constant photosynthetic flux of photons (500 µmol.m^{-2}s^{-1}), instantaneous transpiration (E) and internal CO_2 content (in sub-stomatal chamber) (Ci) were measured on the youngest fully expanded leaf of three plants per treatment using a water vapor analyzer (LCA 2 8.7, ADC, Great Amwell, England) and an air supply unit (ASU 10.87, ADC) set up in series in an open system. The efficiency of the instantaneous carboxylation was calculated as A/Ci according to Zhang et al. (2001) whereas the intrinsic (A/gs) and instantaneous (A/E) water use efficiency were calculated according to de Oliveira et al. (2015). To measure the osmotic potential (Ψs), roots and leaves of three plants per treatment were rapidly rinsed in deionised water, frozen in liquid nitrogen just after harvest. They were then cut in small pieces and placed in a perforated Eppendorf tube which was encased in a second intact tube. After 3 cycles of freeze/thawing, the samples were centrifuged at 15,000 g during 15 min at 4°C. The extracted sap was used to measure the osmolarity (c) using an osmometer with steam pressure Wescor 5500 as described earlier by Lutts et al. (1999). The Ψs was then calculated with the following formula:

$$\Psi s\ (\text{MPa}) = -\ c\ (\text{mosmoles.Kg}^{-1}) \times 2{,}58 \times 10^{-3}$$ according to Van't Hoff equation.

Statistical analysis

For all variables, the data are expressed in the form of mean ± standard error after averaging results over three replications per treatment. Stress effect on a given parameter was performed on the basis of a one-way variance analysis (ANOVA). Means were compared by the Tukey-Kramer test. All analysis was performed with the JMP software (SAS Institute, 2015).

RESULTS AND DISCUSSION

Effects of saline stress on plant growth

Salt stress effects resulted in a decrease of all estimated growth parameters (Table 2). The reduction of growth under salinity in comparison to the control was 20, 17, 22, 39, 32 and 9% with 30 mM NaCl, respectively for the relative shoot height growth (RHG), shoot fresh and dry masses (SFM and SDM), relative root elongation (RRLG), root fresh and dry masses (RFM and RDM). At

Table 2. Effect of different NaCl concentrations on growth parameters of *Amaranthus cruentus* cv. 'Locale' after two weeks stress application. Each value is the mean of three replicates ± S.E.

Parameter	NaCl concentrations (mM)		
	0	30	90
RHG	2.36±0.11[a]	1.89±0.17[a]	1.09±0.20[b]
SFM	34.63±4.24[a]	28.78±6.11[ab]	11.53±1.52[b]
SDM	3.81±0.53[a]	2.98±0.65[ab]	1.46±0.10[b]
RRLR	2.97±0.51[a]	1.83±0.31[a]	1.61±0.28[a]
RFM	12.97±1.89[a]	10.07±2.78[a]	7.82±0.72[a]
RDM	0.693±0.077[a]	0.633±0.075[a]	0.497±0,044[a]

Means followed by the same letter within a line are not significantly different at $P < 0.05$.

90 mM NaCl, reductions matched respectively with 54, 67, 62, 46, 40 and 28% compared to the response of the control for the same parameters. However, the reduction was significant (p<0.05) only for parameters related to aerial part growth at 90 mM NaCl. Thus, NaCl effect resulted mainly in aerial part growth inhibition. Our results indicate that the aerial part was more sensitive to NaCl concentrations than the root system. The growth reduction of aerial part is a common response of glycophyte plant species submitted to salt stress (Abbas et al., 2010; Akram et al., 2012; Acostoa-Motos et al., 2017). Similarly, in diverse amaranth genotypes, it has been reported that the saline constraint reduces aerial part and root growth of plants (Makus, 2003; Omami and Hammes, 2006; Qin et al., 2013; Amukali et al., 2015; Lavini et al., 2016; Wouyou et al., 2017). However, the physiological and biochemical mechanisms responsible for growth reduction are not well clarified to date (Munns and Tester, 2008; Noreen et al., 2010a, b; Ashraf et al., 2011). The biomass reductions in *A. cruentus* under saline conditions are indicative of severe growth limitations. In amaranth, salinity stress negative effects did not affect on the production of biomass but it also negatively affects various morphological parameters as indicated by Wouyou et al. (2017). Bayuelo-Jimenezes et al. (2002) highlighted that salt-tolerant species in the genus *Phaseolus* could maintain a relatively high root growth whenever they are cultivated on salt rich media until 180 mM NaCl. Our results can be explained by a greater ability for osmotic adjustment under stress by the roots as reported in sultana vines under salt stress, particularly at high NaCl concentration (Fisarakis et al., 2001).

Effects of saline stress on physiological parameters

Salt stress induced a significant reduction ($P < 0.05$) of net photosynthesis (*A*) (Figure 2A). Indeed *A* values

decreased from 2.39 µmolCO$_2$ m^{-2}s^{-1} (control) to 1.76 at 30 mM NaCl, and then to 1.16 µmolCO$_2$ m^{-2}s^{-1} under 90 mM NaCl. These values correspond to a reduction of the photosynthetic activity of 26.36 and 51.47% comparatively to control, respectively. The reduction of photosynthetic capacity under salt stress has been reported in numerous species and is considered to be, at least partly, responsible for salt-induced growth reduction (Liu et al., 2011; da Silva, 2011; Saleem et al., 2011; Shahid et al., 2011; Shaheen et al., 2013; R'him et al., 2013). However, according to Omami and Hammes (2006) and Munns and Tester (2008), the effect of salinity on the photosynthetic activity depends upon the salt concentration and the plant species. In *Bruguiera parviflora*, Parida et al. (2002) reported that low levels of salinity even stimulated photosynthesis while high levels clearly reduced it. In our study, a reduction of the photosynthetic activity was observed under all used NaCl concentrations. Omami and Hammes (2006) similarly showed that all NaCl concentrations up to 100 mM NaCl decreased photosynthesis in different amaranth species. We may therefore hypothesize that photosynthesis inhibition is a major component of growth inhibition in *A. cruentus.* The net photosynthesis reduction along with saline stress application would not only be related to the growth reduction (Cramer and Bowman, 1991; Foyer and Noctor, 2005; Passioura and Munns, 2000), but also to an increase in carbohydrate accumulation acting in a negative feed-back (Munns et al., 2000). However, Munns and Tester (2008) considered that it is always difficult to conclude whether a reduction in photosynthetic activity is the cause or the consequence of growth inhibition. Salt stress decreased the intercellular CO_2 concentration (Ci) (Figure 2B) which ranges from (control) 314 to 345 in 30 mM NaCl and 332.67 µmol.mol^{-1} in 90 mM NaCl. The recorded decrease remained however limited from a relative point of view (9.07 and 3.67%, respectively in comparison with the control) and was not significant. In eggplant, Shaheen et al. (2013) found that saline stress did not affect the intercellular CO_2 concentration. In a study carried on two perennial Gramineae species, Liu et al. (2011) found out that in the sensitive species *Eremochloa ophiuroides*, salt stress provoked an increase of the intercellular CO_2 concentration, notably at high NaCl concentrations, whereas in the tolerant species *Paspalum vaginatum*, evolution of intercellular CO_2 concentration was variable depending on stress duration and intensity. In our study, NaCl had no impact on the instantaneous carboxylation efficiency (*A/Ci*) (Figure 2C) ranging from 0.0069 (control) to 0.0057 under 30 mM NaCl and 0.0035 mol.m^{-2}.s^{-1} under 90 mM NaCl. The observed losses correspond respectively to 17.39 and 49.28% reported to the control treatment and might be explained by an inhibition of the carboxylase activity of RubisCO (da Silva et al., 2011).

An inhibition of shoot growth may also lead to
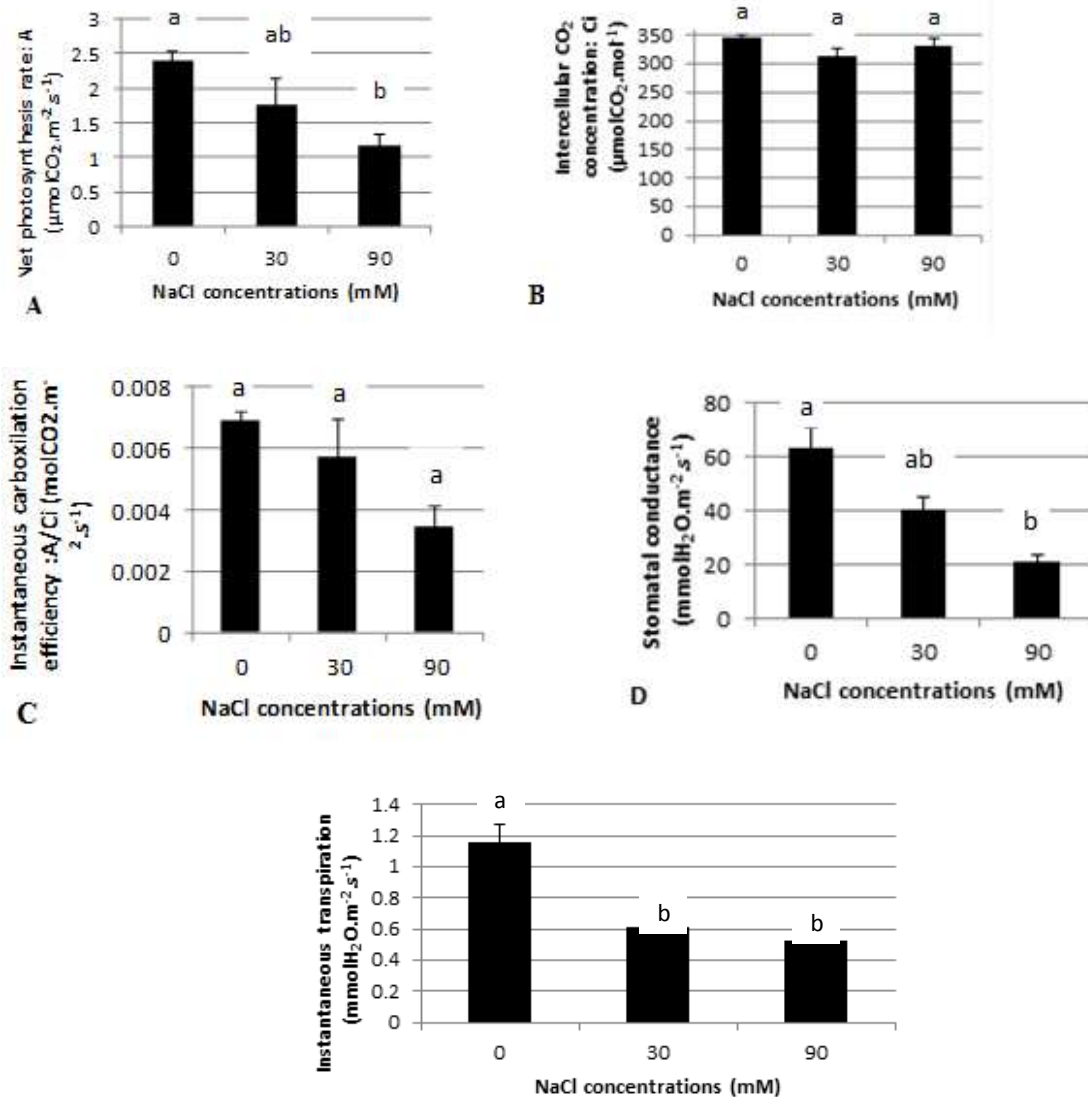
Figure 2. Effect of salinity stress on net photosynthesis rate (A), intercellular CO2 concentration (B) and instantaneous carboxylation efficiency (C), stomatal conductance (D) and instantaneous transpiration (E) of young amaranth plants cv. 'Locale' after two weeks culture on media containing three NaCl concentrations (0, 30 and 90 mM). The vertical bars correspond to the standard errors (n = 3). Averages with different letters are significantly different (p <0.05, or 0.01).

photosynthate accumulation in stressed tissues that would, in turn, generate a feedback signal towards the reduction of photosynthetic activity. The physiological and enzymatic mechanisms implied in these regulations have been questioned in details by Cramer and Bowman (1991), Passioura and Munns (2000), Apel and Hirt (2004), Fricke et al. (2004), Foyer and Noctor (2005), Logan (2005) and Møller et al. (2008). Sobrado (2005) reported that inefficiency of stomatal regulation in stressed plants may directly impair both leaf photosynthetic capacities and biochemical processes. Several works also reported a decrease in chlorophyll content (Koyro 2006; Geissler et al. 2009). The drop of

the chlorophyll"s content could be assigned either to the reduction of its biosynthesis or to a stimulation of chlorophyllase activity (Ashraf and Bhatti 2000). In our study, saline stress induced a significant reduction (p<0.01) of the stomatal conductance (Figure 2D) that was 63.33 (in control), 40.50 (with 30 mM NaCl in the growth media) and 21.17 mmol H_2O m^{-2}s^{-1} (under 90 mM NaCl). Investigating different genotypes of amaranth, Ornami and Hammes (2006) also reported a significant reduction of stomatal conductance. Results presented here matched well with those mentioned earlier in pepper (Lycoskoufis et al., 2005; Niu et al., 2010; R'him et al., 2013) and tomato (Baker and Rosenqvist, 2004).

Table 3. Effect of different NaCl concentrations on shoot water content of *Amaranthus cruentus* cv. 'Locale' after two weeks stress application.

Parameter	NaCl concentrations (mM)		
	0	30	90
Shoot water content (%)	88.93±0.87[a]	89.58±0.56[a]	87.10±0.98[a]

Each value is the mean of three replicates ± S.E. Means followed by the same letter are not significantly different at $P < 0.05$.

Table 4. Effect of saline stress on instantaneous (A/E, $\mu mol_{CO2}.mmol^{-1}_{H2O}$) and intrinsic (A/gs, $\mu mol_{CO2}/mmol^{-1}_{H2O}$) water use efficiency in amaranth young plants of the cultivar 'Locale' after two weeks culture on media containing three NaCl concentrations (0, 30 and 90 mM).

NaCl concentration (mM)	A/E	A/gs
0	2.077±0.097[a]	0.038±0.0026[a]
30	3.252±0.211[ab]	0.068±0.0049[b]
90	4.336±0.556[b]	0.115±0.017[c]

Each value is the mean of three replicates ± S.E. Means followed by the same letter within a column are not significantly different at $P < 0.05$.

Stomatal closure is required for maintenance of water content and could thus be regarded as an adaptive strategy of plants to uphold water whenever facing the osmotic stress under salinity (Shaheen et al., 2013; Davies et al., 2005). This stomata closure might be responsible for the low photosynthetic intensity recorded under salinity conditions. The fact that shoot water content did not change significantly under salt stress (Table 3) supports the hypothesis that stomatal closure efficiently contributes to regulate shoot water content in salt-treated *Amaranthus*.

The effect of salt stress resulted in a significant reduction ($p<0.05$) of instantaneous transpiration (E) (Figure 2E) ranging from 1.16 (without salt stress: control) to 0.61 (by 30 mM NaCl stress) and 0.53 mmol H_2O $m^{-2}s^{-1}$ (under 90 mM NaCl stress), consisting in a reduction of 47.41 and 54.31%, respectively in comparison with the control. In four amaranth genotypes, Ornami and Hammes (2006) observed a decrease in instantaneous transpiration (transpiration rate) of salt-treated plants. A similar tendency has been reported in the genus *Brassica* (Ashraf, 2001). The reduction of instantaneous transpiration observed in our study is obviously the consequence of a decrease in stomatal conductance. Other studies showed that the salt-induced stomatal closure might contribute to avoid the build-up of the toxic ion flux through the transpiration stream (Kerstiens et al., 2002; Vysotskaya et al., 2010). Thus, Koyro (2006) suggested that stomatal conductance reductions represent an adaptive mechanism to face salt excess, reducing the amounts of toxic ions in leaves and thus contributing to avoid premature senescence of photosynthetic tissues.

The effect of salt stress resulted in a significant increase in plant intrinsic (A/gs) ($p<0.001$) and instantaneous (A/E) ($p<0.05$) (Table 4) water use efficiency (WUE). The intrinsic WUE ranged from 0.038 (without salt stress: control) to 0.068 (by 30 mM NaCl stress) and 0.115 $\mu molCO_2/mmolH_2O$ (under 90 mM NaCl stress), consisting in an increase of 78.95 and 202.63%, respectively in comparison with the control; whereas instantaneous WUE ranged from 2.077 (without salt stress: control) to 3.252 (by 30 mM NaCl stress) and 4.336 $\mu molCO_2/mmolH_2O$ (under 90 mM NaCl stress), consisting in an increase of 56.25 and 108.65%, respectively in comparison with the control. Similar results were obtained in *Eugenia myrtifolia* and *Callistemon citrinus* plants submitted to salt stress which were able to increase their intrinsic WUE throughout most of the growing season indicating that the plants maintain higher net photosynthesis rate (A) levels despite reduced stomatal opening (Álvarez and Sánchez-Blanco, 2014; Acosta-Motos et al., 2017).

Salinity induced significant reductions in the leaf and root osmotic potentials ($Ψs$) (Table 5). In leaves, osmotic potential ranged from -1.23 MPa (under 0 mM NaCl) to -1.75 MPa (with 30 mM NaCl) and -3.42 MPa (under 90 mM NaCl stress). In roots, osmotic potential dropped from -0.87 MPa (without salt stress) to -1.35 MPa (with 30 mM NaCl) and -2.14 MPa (under 90 mM NaCl). It is well known that the presence of salt excess in rhizosphere leads to reductions in osmotic potential and consequently, contributes to the decrease in plant water potential (Sánchez-Blanco et al., 2004; Munns, 2005; Franco et al,. 2011). Our results are in agreement with those reported earlier in sunflower (Akram et al., 2012),

Table 5. Effect of saline stress on osmotic potential (Ψs) of leaves and roots measured at amaranth young plants of the cultivar 'Locale' after two weeks culture on media containing three NaCl concentrations (0, 30 and 90 mM).

NaCl concentration (mM)	Leaves	Root
0	-1.23±0.11[a]	-0.87±0.14[a]
30	-1.75±0.10[b]	-1.35±0.04[ab]
90	-3.42±0.31[b]	-2.14±0.28[b]

Each value is the mean of three replicates ± S.E. Means followed by the same letter within a column are not significantly different at $P < 0.05$.

pea (Noreen et al., 2010a) and radish (Noreen et al., 2012). Munns and Tester (2008) and Noreen et al. (2010a, b) explained this reduction of leaf osmotic potential by a loss of water, an increase in the uptake of dissolved ions or an oversynthesis of compatible organic compounds. In our study, the reduction of osmotic potential could not be explained by a decrease in water content since no significant reduction of shoot water content occurred under the NaCl concentrations used (Table 2). Thus, it is more likely that the reduction of osmotic potential under salinity stress may be due to an increase in ion absorption and/or the oversynthesis of soluble organic compounds. Na^+ and/or Cl^- ions are known to increase considerably in saline stress conditions in numerous plant species including lentil (Ashraf and Waheed, 1993), corn (Cramer et al., 1994), rice (Lutts et al., 1996), cotton (Chen and Zhao, 1996; Leidi and Saiz, 1997), durum wheat (Almansouri et al., 1999); sugarcane (Akhtar et al., 2003; Wahid, 2004; Gandonou et al., 2011) and *A. cruentus* (Wouyou, 2017). Considering their putative toxicities, most of these ions are thought to be sequestered within vacuoles and additional organic compounds such as proline or sugars, or non-toxic ions such as K^+ ensure osmotic adjustment in the cytosol.

Conclusion

The reduction of plant growth under salt stress is due to a loss in photosynthetic activity mostly related to stomatal closure. The maintenance of high water use efficiency appeared as an important strategy to face salt stress in *A. cruentus*. The results exposed here provide specific physiological cues for improvement of salt-tolerance in amaranth.

ACKNOWLEDGEMENTS

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

REFERENCES

Abbas W, Ashraf M, Akram NA (2010). Alleviation of salt-induced adverse effects in eggplant (*Solanum melongena* L.) by glycine betaine and sugarbeet extracts. Scientia Horticulturae 125: 188-195.

Acosta-Motos JR, Ortuño MF, Bernal-Vicente A, Diaz-Vivancos P, Sanchez-Blanco MJ, Hernandez JA (2017). Plant responses to salt stress: Adaptive Mechanisms. Agronomy pp. 1-38.

Akhtar S, Wahid A, Rasul E (2003). Emergence, growth and nutrient composition of sugarcane sprouts under NaCl salinity. Biologia Plantarum 46(1):113-116.

Akram NA, Ashraf M, Al-Qurainy F (2012). Aminolevulinic acid-induced changes in some key physiological attributes and activities of antioxidant enzymes in sunflower (*Helianthus annuus L.*) plants under saline regimes. *Scientia Horticulturae* 142:143-151.

Allemann J, Van Den Heever E, Viljoen J (1996). Evaluation of Amaranthus as a possible vegetable crop. Applied Plant Science 10:1-4.

Almansouri M, Kinet JM, Lutts S (1999). Compared effects of sudden and progressive impositions of salt stress in three Durum wheat (*Triticum durum* Desf.) cultivars. Journal of Plant Physiology 154:743-752.

Álvarez S, Gómez-Bellot MJ, Castillo M, Bañón S, Sánchez-Blanco MJ (2012). Osmotic and saline effect on growth, water relations, and ion uptake and translocation in *Phlomis purpurea* plants. Environmental and Experimental Botany 78:138-145.

Álvarez S, Sánchez-Blanco MJ (2014). Long-term effect of salinity on plant quality, water relations, photosynthetic parameters and ion distribution in *Callistemon citrinus*. Plant Biology 16:757-764.

Amukali O, Obadoni BO, Mensah JK (2015). Effects of different NaCl concentrations on germination and seedlings growth of *Amaranthus hybridus* and *Celosia argentea.* African Journal of Environmental Science and Technology 9:301-306.

Apel K, Hirt H (2004). Reactive oxygen species: metabolism, oxidative stress and signal transduction. Annual Review of Plant Biology 55:373-99.

Ashraf M (2001). Relationships between growth and gas exchange characteristics in some salt-tolerant amphidipoid *Brassica* species in relation to their diploid parents. Environmental and Experimental Botany 45:155-163.

Ashraf M, Akram NA, Al-Qurainy F, Foolad MR (2011). Drought tolerance: roles of organic osmolytes, growth regulators and mineral nutrients. In Advances in Agronomy Academic Press 111:249-296.

Ashraf M, Harris JC (2004). Potential biochemical indicators of salinity tolerance in plants. Plant Science 166:3-16.

Ashraf M, Waheed A (1993). Responses of some local/exotic accessions of lentil (*Lens culinaris* Medic.) to salt stress. Journal of Agronomy and Crop Science 170:103-112.

Ashraf MY, Bhatti AS (2000). Effect of salinity on growth and chlorophyll

content in rice. Pakistan Journal of Scientific and Industrial Research 43:130-131.

Baker NR, Rosenqvist E (2004). Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. Journal of Experimental Botany 55:1607-1621.

Bayuelo-Jiménes JS, Debouck DG, Lynch JP (2002). Salinity tolerance of *Phaseolus* species during early vegetative growth. Crop Science 42:2184-2192.

Bhattacharjee S (2008). Triadimefon pretreatment protects newly assembled membrane system and causes up-regulation of stress proteins in salinity stressed *Amaranthus lividus* L. during early germination, Journal of Environmental Biology 29(5):805-810.

Brugnoli E, Lauteri M (1991). Effects of salinity on stomatal conductance, photosynthetic capacity, and carbon isotope discrimination of salt-tolerant (*Gossypium hirsutum* L.) and salt-sensitive (*Phaseolus vulgaris* L.) C3 non-halophytes. Plant Physiology 95:628-635.

Chaves MM, Flexas J, Pinheiro C (2009). Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Annnals of Botany 103: 551-560.

Chen XL, Zhao KF (1996). Effect of NaCl stress on germination of maize and the alleviation of exogenous Ca^{2+}. Acta Agriculturae Boreali-Sinica 11:89-92.

Cramer GR, Alberico GJ, Schidt C (1994). Salt tolerance is not associated with the sodium accumulation of two maize hydrids. Australian Journal of Plant Physiology 21:675-692.

Cramer GR, Bowman DC (1991). Kinetics of maize leaf elongation. I. Increased yield threshold limits short-term, steady-state elongation rates after exposure to salinity. Journal of Experimental Botany 42:1417-1426.

Cunningham AB, Dejager PJ, Hansen LCB (1992). The indigenous plant use programme. Foundation for Research Development, Pretoria.

da Silva EN, Ribeiro RV, Ferreira-Silva SL, Viégas RA, Silveira JAG (2011). Salt stress induced damages on the photosynthesis of physic nut young plants. Scientia Agricola 68:62-68.

Davies WJ, Kudoyarova G, Hartung W (2005). Long-distance ABA signaling and its relation to other signaling pathways in the detection of soil drying and the mediation of the plant's response to drought. Journal of plant growth regulation 24:285-295.

Delfine S, Alvino A, Zacchini M, Loreto F (1998). Consequences of salt stress on conductance to CO_2 diffusion, Rubisco characteristics and anatomy of spinach leaves. Australian Journal of Plant Physiology 25:395-402.

Fisarakis I, Chartzoulakis K, Stavrakas D (2001). Response of sultana vines (*V. vinifera* L.) on six rootstocks to NaCl salinity exposure and recovery. Agricultural Water Management 51:13-27.

Foyer CH, Noctor G (2005). Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant, Cell and Environment 28:1056-1071.

Franco JA, Bañón S, Vicente MJ, Miralles J, Martínez-Sánchez JJ (2011). Root development in horticultural plants grown under abiotic stress conditions- A review. Journal of Horticultural Science and Biotechnology 86:543-556.

Fricke W, Akhiyarova G, Veselov D, Kudoyarova G (2004). Rapid and tissue-specific changes in ABA and in growth rate response to salinity in barley leaves. Journal of Experimental Botany 55:1115-1123.

Gandonou CB, Bada F, Gnancadja SL, Abrini J, Skali Senhaji N (2011). Effects of NaCl on Na^+, Cl^- and K^+ ions accumulation in two sugarcane (*Saccharum sp.*) cultivars differing in their salt tolerance, International Journal of Plant Physiology and Biochemistry 3(10):155-162.

Geissler N, Hussin S, Koyro HW (2009). Elevated atmospheric CO_2 concentration ameliorates effects of NaCl salinity on photosynthesis and leaf structure of *Aster tripolium* L. Journal of Experimental Botany 60:137-151.

Hussain K, Majeed A, Nawaz K, Khizar HB, Nisar MF (2009). Effect of different levels of salinity on growth and ion contents of black seeds (*Nigella sativa* L.). Current Research Journal of Biological Sciences 1:135-138.

Jaleel CA, Manivannan P, Sankar B (2007). Induction of drought stress

tolerance by ketoconazole in *Catharanthus roseus* is mediated by enhanced antioxidant potentials and secondary metabolite accumulation. Colloids and surfaces B: Biointerfaces 60:201-206.

James RA, Rivelli AR, Munns, R, von Caemmerer S (2002). Factors affecting CO2 assimilation, leaf injury and growth in salt-stressed durum wheat. Functional Plant Biology 29:1393-1403.

Kerstiens G, Tych W, Robinson MF, Mansfield TA (2002). Sodium-related partial stomatal closure and salt tolerance of Aster tripolium. New Phytologist 153:509-515.

Koyro HW (2006). Effect of salinity of growth, photosynthesis, water relations and solute composition of the potential cash crop halophyte *Plantago coronopus* (L.). Environmental and Experimental Botany 56:136-146.

Lavini A, Pulvento C, d'Andria R, Riccardi M (2016). Effects of saline irrigation on yield and qualitative characterization of seed of an amaranth accession grown under Mediterranean conditions. The Journal of Agricultural Science 154(5):858-869.

Lee GJ, Carrow RN, Duncan RR (2004). Photosynthetic responses of salinity stress of halophytic seashore *Paspalum* ecotypes. Plant Science 166:1417-1425.

Leidi EO, Saiz JF (1997). Is salinity tolerance related to Na accumulation in Upland cotton (*Gossypium hirsutum*) seedlings? Plant and Soil 190:67-75.

Liu Y, Du H, Wang K, Huang B, Wang Z (2011). Differential photosynthetic responses to salinity stress between two perennial grass species contrasting in salinity tolerance. HortScience 46(2):311-316.

Logan BA (2005). Reactive oxygen species and photosynthesis. In *Antioxidants and Reactive Oxygen Species in Plants*, ed. N Smirnoff. Oxford: Blackwell pp. 250-267.

Lutts S, Bouharmont J, Kinet J.M (1999). Physiological characterization of salt-resistant rice (*Oryza sativa*) somaclones. Australian Journal of Botany 47:835-849.

Lutts S, Kinet JM, Bouharmont J (1996). Effects of salt stress on growth, mineral nutrition and proline accumulation in relation to osmotic adjustment in rice (*Oryza sativa* L.) cultivars differing in salinity resistance. Plant Growth Regulation 19:207-218.

Lycoskoufis IH, Savvas D, Mavrogianopoulos G (2005). Growth, gas exchange, and nutrient status in pepper (*Capsicum annuum* L.) grown in recirculating nutrient solution as affected by salinity imposed to half of the root system. Scientia Horticulturae 106:147-161.

Makus DJ (2003). Salinity and Nitrogen Level Affect Agronomic Performance, Leaf Color and Leaf Mineral Nutrients of Vegetable Amaranth. Subtropical Plant Science 55:1-6.

Megdiche W, Hessini K, Gharbi F, Jaleel CA, Ksouri R, Abdelly C (2008). Photosynthesis and photosystem-efficiency of two salt adapted halophytic seashore *Cakile maritima* ecotypes. Photosynthetica 46:410-419.

Munns R (2002). Comparative physiology of salt and water stress. Plant, Cell and Environment 25: 239-250.

Munns R (2005). Genes and salt tolerance: Bringing them together. Plant phytology 167:645-663.

Munns R, Guo J, Passioura JB, Cramer GR (2000). Leaf water status controls day-time but not daily rates of leaf expansion in salt-treated barley. Australian Journal of Plant Physiology 27:949-957.

Munns R, James RA, Laüchli A (2006). Approaches to increasing the salt tolerance of wheat and other cereals. Journal of Experimental Botany 57:1025-1043.

Munns R, Tester M (2008). Mechanisms of salinity tolerance. Annual Review of Plant Biology 59:651-681.

Niu G, Rodriguez DS, Starman T (2010). Response of bedding plants to saline water irrigation. HortScience 45 (4): 628-636.

Noreen Z, Ashraf M, Akram NA (2010a). Salt-induced modulation in some key physio-biochemical processes and their use as selection criteria in potential vegetable crop pea (*Pisum sativum* L.). Crop Pasture Science 61:369-378.

Noreen Z, Ashraf M, Akram NA (2010b). Salt-induced regulation of some key antioxidant enzymes and physio-biochemical phenomena in five diverse cultivars of turnip (*Brassica rapa* L.). Journal of Agronomy and Crop Science 196:273-285.

Noreen Z, Ashraf M, Akram NA (2012). Salt-induced regulation of

photosynthetic capacity and ion accumulation in some genetically diverse cultivars of radish (*Raphanus sativus* L.). Journal of Applied Botany and Food Quality 85:91-96.

Ornami EN, Hammes PS (2006). Ameliorative effects of calcium on growth and mineral uptake of salt-stressed amaranth, South African Journal of Plant and Soil 23(3):197-202.

Parida A, Das AB, Das P (2002). NaCl stress causes changes in photosynthetic pigments, proteins, and other metabolic components in the leaves of a true mangrove, *Bruguiera parviflora*, in hydroponic cultures. Journal of Plant Biology 45:28-36.

Passioura JB, Munns R (2000). Rapid environmental changes that affect leaf water status induce transient surges or pauses in leaf expansion rate. Australian Journal of Plant Physiology 27:941-948.

Passioura JB (2010). Scaling up: The essence of effective agricultural research. Functional Plant Biology 37: 585-591.

Prakash OM, Zaidi PH (2000). Effect of amaranth *(Amaranthus spinosus* L.) supplemented maize diet on blood haemoglobin and lipid metabolism in rats. Annals of Agricultural Research 21(2):223-232.

Qin L, Guo S, Ai W, Tang Y, Cheng Q, Chen G (2013). Effect of salt stress on growth and physiology in amaranth and lettuce: Implications for bioregenerative life support system. Advances in Space Research 51:476-482.

R'him T, Tlili I, Hnan I, Ilahy R, Benali A, R'him JH (2013). Effet du stress salin sur le comportement physiologique et métabolique de trois variétés de piment (*Capsicum annuum* L.). Journal of Applied Biosciences 66:5060-5069.

Sánchez-Blanco MJ, Rodríguez P, Morales MA, Ortuño MF, Torrecillas A (2002). Comparative growth and water relations of *Cistus albidus* and *Cistus monspeliensis* plants during water deficit conditions and recovery. Plant Science 162:107-113.

Sánchez-Blanco MJ, Rodríguez P, Olmos E, Morales MA, Torrecillas A (2004). Differences in the effects of simulated sea aerosol on water relations, salt content, and leaf ultrastructure of rock-rose plants. Journal of Environmental Quality 33:1369-1375.

SAS Institute (2015). SAS/STAT user's guide, Vol. 1; Release 6.03, ed. SAS Institute Inc. Cary, NC. USA.

Shaheen S, Naseer S, Ashraf M, Akram AN (2013). Salt stress affects water relations, photosynthesis, and oxidative defense mechanisms in *Solanum melongena* L. Journal of Plant Interactions 8(1):85-96.

Shahid MA, Pervez MA, Balal RM, Ahmad R, Ayyub CM, Abbas T, Akhtar N (2011). Salt stress effects on some morphological and physiological characteristics of okra (*Abelmoschus esculentus* L.). Soil and Environment 30(1):66-73.

Shannon MC, Grieve CM (1999). Tolerance of vegetable crops to salinity. Scientia horticulturae 78:5-38.

Sobrado MA (2005). Leaf characteristics and gas exchange of the mangrove *Laguncularia racemosa* as affected by salinity. Photosynthetica 43:217-221.

Stoeva N, Kaymakanova M (2008). Effect of salt stress on the growth and photosynthesis rate of bean plants. Journal of Central European Agriculture 9:385-392.

Villa-Castorena M, Ulery AL, Catalan-Valencia EA, Remmenga MD (2003). Salinity and nitrogen rate effects on the growth and yield of Chile pepper plants. Soil Science Society of America Journal 67:1781-1789.

Vysotskaya L, Hedley PE, Sharipova G, Veselov D, Kudoyarova G, Morris J, Jones HG (2010). Effect of salinity on water relations of wild barley plants differing in salt tolerance. AoB Plants 86:407-421.

Wahid A (2004). Analysis of toxic and osmotic effects of sodium chloride on leaf growth and economic yield of sugarcane. Botanical Bulletin of Academia Sinica 45:133-141.

Went FE (1957). The experimental control of plant growth, Chronica Botanica Co. Ronald Press Co; Waltham M, n° 17: 343 p. New York.

Wouyou DA (2017). Réponse de l'amarante (*Amaranthus cruentus,* l.) au stress salin: caractérisation de cultivars, mécanisme physiologique de résistance et qualité nutritionnelle des feuilles, thèse de doctorat, Université d'Abomey-Calavi, Décembre 2017, 155 p.

Wouyou A, Gandonou CB, Montcho D, Kpinkoun J, Kinsou E, Assogba Komlan F, Gnancadja LS (2016). Salinity resistance of six Amaranth (*Amaranthus* sp.) cultivars cultivated in Benin at germination stage. International Journal of Plant and Soil Science 11(3):1-10.

Wouyou A, Gandonou CB, Assogba-Komlan F, Montcho D, Zanklan AS, Lutts S, Gnancadja SL (2017). Salinity resistance of five amaranth (*Amaranthus cruentus*) cultivars at young plant stage. International Journal of Plant and Soil Science 14:1-11.

Zhang S, Li Q, Ma K, Chen L (2001). Temperature-dependent gas exchange and stomatal/nonstomatal limitation to CO_2 assimilation of *Quercus liaotungensis* under midday higher irradiance. Photosynthetica 39:383-388.