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NaCl and Na_2SO_4 Salinities Have Different Impact on Photosynthesis and Yield-Related Parameters in Rice (*Oryza sativa* L.)

Willy Irakoze [1,2,*], Hermann Prodjinoto [1], Séverin Nijimbere [2], Gervais Rufyikiri [3] and Stanley Lutts [1,*]

[1] Groupe de Recherche en Physiologie végétale, Earth and Life Institute–Agronomy (ELIA) Université catholique de Louvain, 5 (bte 7.07.13) Place Croix du Sud, 1348 Louvain-la-Neuve, Belgium; hermann.prodjinoto@uclouvain.be

[2] Faculté d'Agronomie et de Bio-ingénierie, Université du Burundi, Bujumbura 2940, Burundi; niseverino@yahoo.fr

[3] Geneva Centre for Security Policy (GCSP), 1211 Geneva, Switzerland; grufyikiri@yahoo.fr

* Correspondence: w_irakoze@yahoo.com (W.I.); stanley.lutts@uclouvain.be (S.L.); Tel.: +257-79840048 (W.I.); +32-10472037 (S.L.)

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Abstract: To elucidate the comparative effect of chloride and sulfate salinities on photosynthesis and yield components in rice, plants of *Oryza sativa* (cv. I Kong Pao (salt-sensitive)) were exposed in nutrient solutions to 20 mM Na_2SO_4 or 40 mM NaCl (electrical conductivity of c.a. 4.30 dS m^{-1} for both solutions) from seedlings to maturity stage. Both types of salt induced a strong decrease in net photosynthesis (A_N) at the seedling and tillering stages, while the intercellular CO_2 concentrations (Ci) remained unaffected. Instantaneous transpiration (E) and stomatal conductance (g_s) decreased at the tillering and seedling stages, respectively, only in plants exposed to NaCl. Chloride salinity also strongly decreased photosynthetic pigments, while no impact was detected in response to Na_2SO_4. All yield-related parameters were affected by salinities, but NaCl was significantly more deleterious than Na_2SO_4 for the mean number of tillers produced per plant, spikelets sterility and non-viable pollen percentage. In contrast, both types of salinity similarly impacted the percentage of fertile tillers and 1000-grain weight. At the grain level, more than 90% of toxic ions (Na^+, excess of Cl^- and S^{6+}) accumulated in the hulls, thus preserving the internal part of the caryopses from toxic ion injuries.

Keywords: chloride; sulfate; salinity; *Oryza sativa*; photosynthesis; yield

1. Introduction

Soil salinity is a major environmental constraint to crop production, affecting millions of hectares of land throughout the world, and costing billions of dollars every year. High contents of soluble salts in the soil are reported in numerous areas of the world. Soil salinity is aggravated by secondary salinization, due to irrigation with low quality water. On a long-term basis, global warming and the rising sea level will undoubtedly contribute to salinization in coastal areas [1,2].

Rice (*Oryza sativa* L.) is extremely sensitive to salinity and yield decreases by more than 10% for every unit (dS/m) increase in electrical conductivity of root-zone saturated soil extract above 3 dS/m [3]. Salt sensitivity depends on the plant developmental stage. In *Oryza sativa*, early seedling growth and reproductive stages are the most salt-sensitive stages [4–8]. Numerous authors reported that salinity delays flowering in rice and has a negative impact on several yield components, including the number of panicles, fertile tillers and spikelets per plant, floret fertility and grain size [7,9–13]. Differential sensitivity during developmental stage is a major issue in the management of saline water for irrigation

and Zeng et al. The authors of [13] demonstrated that salinity has a different impact if applied at booting stage or at the panicle initiation stage. In numerous rice production systems, however, salinity is present during most of the plant developmental cycle. As a consequence, the ultimate consequence of salinity on rice yield not only depends on salt impact on the reproductive phase of development, but is also influenced by stand establishment and the impact of photosynthesis during the vegetative stage, since pre-anthesis assimilates will be subsequently translocated during grain filling [11,14,15].

Salt stress involve two distinct components. The first component is the so called "osmotic effect", which is due to a salt-induced decrease in the osmotic potential of the soil solution, and which hampers water uptake by the roots [16,17]. The second component of salinity is the "ionic effect", and is due to the internal accumulation of toxic ions, leading to tissue necrosis and early leaf senescence [18]. Studying the effect of NaCl salinity on photosynthesis and dry matter accumulation in developing rice grains, Sultana et al. [11] concluded that reduction in photosynthesis in the salinized rice plant depended not only on a reduction of available CO_2 by stomatal closure, but also on the cumulative effects of biochemical alterations, photosynthetic pigments degradation and structural modifications of chloroplasts. Castillo et al. [19] compared the effect of salt and iso-osmotic concentration of polyethylene glycol in two contrasted rice cultivars, and concluded that the plant response was mainly attributed to the osmotic component of salt stress. In contrast, Khatun and Flowers [20] concluded that accumulation of Na^+ and Cl^- excess are responsible for salt-induced decrease in pollen viability and stigma receptivity.

Most studies dealing with salt stress focus on NaCl. In field conditions, however, high soil electrical conductivity often results from a complex mixture of various ions, including not only Na^+ and Cl^-, but also Ca^{2+} and SO_4^{2-} [1,21]. Some studies are dealing with realistic conditions and consider a mixture of various salts [3,10,22], but only few works discriminated the specific impacts of the various ions [23,24]. Recently, Irakoze et al. [25] found that NaCl in young seedlings of rice was more toxic than Na_2SO_4, and that sodium and proline accumulation were higher in NaCl-treated plants than in those exposed to Na_2SO_4, while shoot osmotic potential exhibited an inverse trend. Unfortunately, no data are available regarding the differential impacts of the two salts on yield-related parameters. Since Zhu et al. [7] demonstrated that leaf K^+/Na^+ ratio quantified under stress conditions at the vegetative stage may be used as a predictive criterion for yield-potential in several rice cultivars, we hypothesize that sodium iso-molar solutions of NaCl would be more detrimental to yield than Na_2SO_4.

An experiment was therefore performed in nutrient solutions containing 20 mM Na_2SO_4 or 40 mM NaCl. It confirms that NaCl was more toxic than Na_2SO_4 for most yield-related parameters, and that the two types of salinity differently affected leaf photosynthesis and the efficiency of the reproductive structures.

2. Materials and Methods

2.1. Plant Material and Growing Conditions

Seeds of the rice cultivar I Kong Pao (IKP; salt-sensitive) were obtained from the International Rice Research Institute (IRRI; Philippines). Seeds were germinated on two layers of filter paper (Whatman No. 2), moistened with 10 mL of sterile deionized water in a growth chamber at 25 °C, under a 12 h daylight period (120 µmol m^{-2} s^{-1}). Ten-day-old seedlings were transferred into a greenhouse and were fixed on polystyrene plates floating on Yoshida nutritive solution [26]. Illumination was provided by LED LumiGrow Lights (650 W, red-blue) for 12 h d^{-1} at a photon flux density (PAR) of 150 µmoles m^{-2} s^{-1}. Daytime humidity was between 70% and 80%, and the temperature was maintained at 28 °C during the day and 26 °C during the night. For each treatment, the seedlings were distributed among three tanks (twenty seedlings per tank) containing 50 l of solution. The solutions were renewed weekly and tanks were randomly rearranged in the greenhouse. After two weeks of acclimatization in control conditions, the seedlings were exposed to 20 mM Na_2SO_4 or 40 mM NaCl (electrical conductivity of

c.a. 4.30 dS m^{-1} for both solutions; Ψs = −0.088 MPa for control, −0.30 MPa for 40 mM NaCl and −0.22 MPa for 20 mM Na_2SO_4), until the maturity stage.

At the end of the experiment, three plants were tagged in each of the three replicate treatments. The number of tillers per plant and spikelets per panicle, the percentage of floret sterility and fertile tillers per plant as well as the 1000-grains weight were recorded from these samples.

2.2. Estimation of Pollen Viability and Grain Ion Content

Pollen viability was estimated using the staining procedure of Alexander [27]. Pollen was collected immediately after anthesis in at least 10 spikelets from the central part of the main panicle, and treated in a drop of freshly staining solution. The staining of 200–300 pollen grains from three individual panicles from each of three plants per treatment was observed under a microscope.

The measurements of the ion content were performed on mature grains (considering separately husks (lemmas and paleas) and dehusked grains): 20 mg DW were crushed in powder and digested with nitric acid (68%) at 80 °C. After complete evaporation, the residues were dissolved with HNO_3 (68%) + HCl_{cc} (1:3, *v/v*). The solution was filtered using a layer of Whatman (85 mm, Grade 1). The filtrate was used to determine the cations concentration (K^+, Na^+, S^{6+}) by flame emission, using an atomic absorption spectrometer (Thermo scientific S series model AAS4). Chloride was specifically extracted according to Hamrouni et al. [28]. Anions (Cl^-) were quantified by liquid chromatography (HPLC-Dionex ICS2000).

2.3. Photosynthesis-Related Parameters

Photosynthesis-related parameters were estimated at the seedling stage (14 days after stress imposition) and at the tillering stage (45 days after stress imposition). The leaf n°3 (blade fully unfolded) from the top of the plant (basipedal numbering) was selected for measurements. At the tillering stage, only the main stem was considered.

Gas exchange was recorded with an infrared gas analyzer (LCA4; ADC Bioscientific, Hoddesdon, Hertfordshire, UK) and an air supply unit (ASU 10.87, ADC, Herstshire, UK). Gas exchange was first measured using a PLC Parkinson leaf cuvette on intact leaves for 1 min (20 records/min), and an air flow of 300 mL/min on a leaf portion of 6.25 cm^2. The photosynthetic flux density (PPFD) at the leaf surface was set to 500 $\mu mol.m^{-2}.s^{-1}$, while temperature and humidity were set at 25 °C and 75%, respectively. In order to partly saturate the carboxylation sites, a CO_2 molar ratio high enough to quantify the impact of salts on the biochemical processes of photosynthesis independently of stomatal closure was used, and air jets of 800 $\mu mol.mol^{-1}$ CO_2 and 2% O_2 in N_2 were directed at both surfaces. The net photosynthetic rate in near-saturating conditions (A_N), the instantaneous transpiration rate (E) and the intercellular CO_2 concentration (C_i) were estimated on the third leaf at the vegetative stage, as well as on the flag leaf on the reproductive one, since photosynthesis of the flag leaf provides the majority of sugars translocated to the grain. Instantaneous water use efficiency (WUE) was estimated by the A_N/E ratio. Six plants were considered for each treatment, and all measurements were performed between 9:00 and 11:00 am. Stomatal conductance (g_s) was measured on the same leaves, using a porometer (AP4, Delta-T Devices, Cambridge, UK).

Chlorophyll a (*Chl* a), chlorophyll b (*Chl* b) and carotenoid were extracted from the leaves in 80% cold acetone. The *Chl* a, *Chl* b and carotenoid concentrations were determined by spectrophotometry, according to the procedure described by Lichtenthaler [29], and using the following equations:

$$\textit{Chl}\ \text{a (mg/l)} = (12.25 \times \text{A663.2}) - (2.79 \times \text{A646.8})$$

$$\textit{Chl}\ \text{b (mg/l)} = (21.50 \times \text{A646.8}) - (5.10 \times \text{D663.2})$$

$$\text{Carotenoid (mg/l)} = [(1000 \times \text{A470}) - (1.82 \times \text{Chl a}) - (85.02 \times \text{Chl b})]/198$$

2.4. Statistical Treatment of the Data

The experiment was performed three times independently from 2016 to 2019, and provided similar trends. The results presented hereafter are from one single representative experiment. Statistical analyses were performed using JMP Pro 13 software. Mean values and standard error (SE) were obtained from 6 replicates for photosynthesis-related parameters, except the pigments content parameter, where 3 replicates were considered as yield components. Mean values and SE were analyzed using Tukey's HSD all-pairwise comparisons as a post-hoc test and a P value < 0.05 was considered to be statistically significant. A one-way analysis of variance (ANOVA) was performed for the yield components and pigments content parameters, whereas, for the photosynthesis-related parameters, a two-way ANOVA was performed to detect growth stage, treatment and their interaction effects. The graphs were plotted using SigmaPlot 10.0 software.

3. Results

All plants remained alive until the end of the treatment. Net photosynthesis (Figure 1) was lower at the tillering than at the seedling stage. At the two developmental stages, NaCl and Na_2SO_4 induced a similar decrease in A_N. In contrast, Ci values were not affected by salinities, and remained similar at the two developmental stages. Instantaneous transpiration decreased at the tillering stage for plants exposed to NaCl salinity, but not for control or plants exposed to Na_2SO_4. Both types of salinities induced a similar decrease in E values. At the seedling stage, stomatal conductance was reduced in response to NaCl only, while both types of salinity reduced g_s at the tillering stage. The water use efficiency remained unaffected by salinities, but decreased at the tillering comparatively to the seedling stage (Table 1).

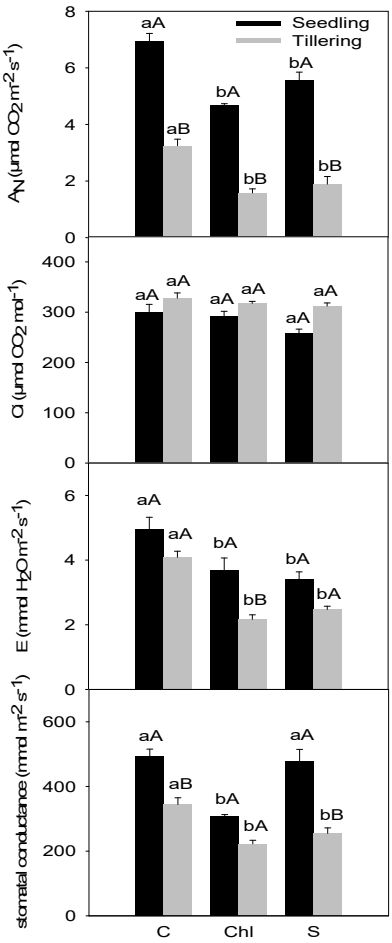

Figure 1. Effects of salinity stress application on mean net photosynthetic rate (A_N), intercellular CO_2 concentration (C_i), instantaneous transpiration rate (E) and stomatal conductance of I Kong Pao (IKP)

rice cultivar grown in the Yoshida nutrient solution without salt stress (C), with 40 mM NaCl (Chl) or 20 mM Na_2SO_4 (S). Each value is the mean of six replicates per treatment and vertical bar is standard error of mean. Treatments followed by the same lower-case letter for a particular vegetative stage do not differ statistically. Vegetative stage followed by the same upper-case letter in a particular treatment do not differ statistically.

Table 1. Water use efficiency (WUE) measured at seedling and tillering stages of IKP rice cultivar grown in Yoshida nutrient solution without salt stress (C), with 40 mM NaCl (Chl) or 20 mM Na_2SO_4 (S).

mmol CO_2 Uptake/mmol H_2O Loss						
	Seedling			**Tillering**		
	C	**Chl**	**S**	**C**	**Chl**	**S**
WUE	1.4 ± 0.09 ^{aA}	1.3 ± 0.14 ^{Aa}	1.6 ± 0.12 ^{aA}	0.8 ± 0.08 ^{aB}	0.7 ± 0.09 ^{aB}	0.8 ± 0.08 ^{aB}

Treatments followed by the same lower-case letter for a particular vegetative stage do not differ statistically. Vegetative stage followed by the same upper-case letter in a particular treatment do not differ statistically.

At the seedling stage, chloride salinity induced a strong decrease in *Chl* a, *Chl* b and carotenoids content (Figure 2) while Na_2SO_4 had no impact on the photosynthetic pigment concentration. At the tillering stage, chloride salinity reduced *Chl* a and carotenoids, while Na_2SO_4, once again, had no significant impact on the pigment content. The *Chl* a/*Chl* b ratio increased in rice seedlings exposed to NaCl.

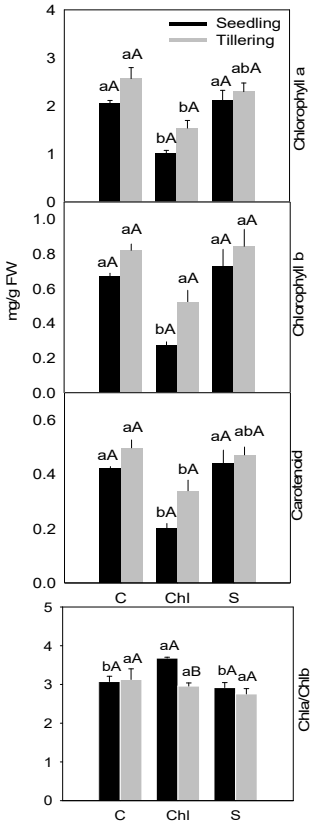

Figure 2. Effects of salinity stress application on chlorophyll and carotenoids content of IKP rice cultivar grown in the Yoshida nutrient solution without salt stress (C), with 40 mM NaCl (Chl) or 20 mM Na_2SO_4 (S). Each value is the mean of three replicates per treatment and vertical bar is standard error of mean. Treatments followed by the same lower-case letter for a particular vegetative stage do not differ statistically. Vegetative stage, followed by the same upper-case letter in a particular treatment, do not differ statistically.

Net photosynthesis of the flag leaf was strongly reduced by both NaCl and Na_2SO_4 (Figure 3), the minimal value being reported in response to NaCl, although the difference between the types of salt was not significant. All plants flowered, and no delay in flowering was recorded for stressed plants (detailed data not shown).

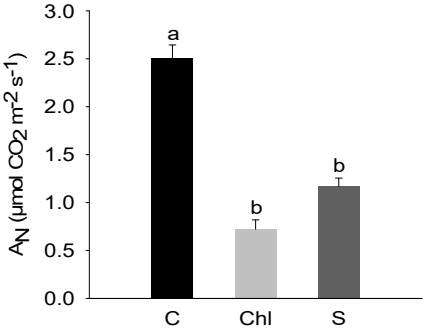

Figure 3. Effects of salinity stress application on mean net photosynthetic rate (A_N) measured on the flag leaf of IKP rice cultivar grown in the Yoshida nutrient solution without salt stress (C), with 40 mM NaCl (Chl) or 20 mM Na_2SO_4 (S). Means with similar letters are not different at $p < 0.05$, according to Tukey's multiple range test at 95%.

All yield-related parameters were affected by salinities (Figure 4). The deleterious impact of NaCl was higher than the impact of Na_2SO_4 for the mean number of tillers produced per plant, spikelets sterility and non-viable pollen percentage, while both types of salinity had a similar impact on tiller fertility, 1000-grain weight and spikelet number per panicle.

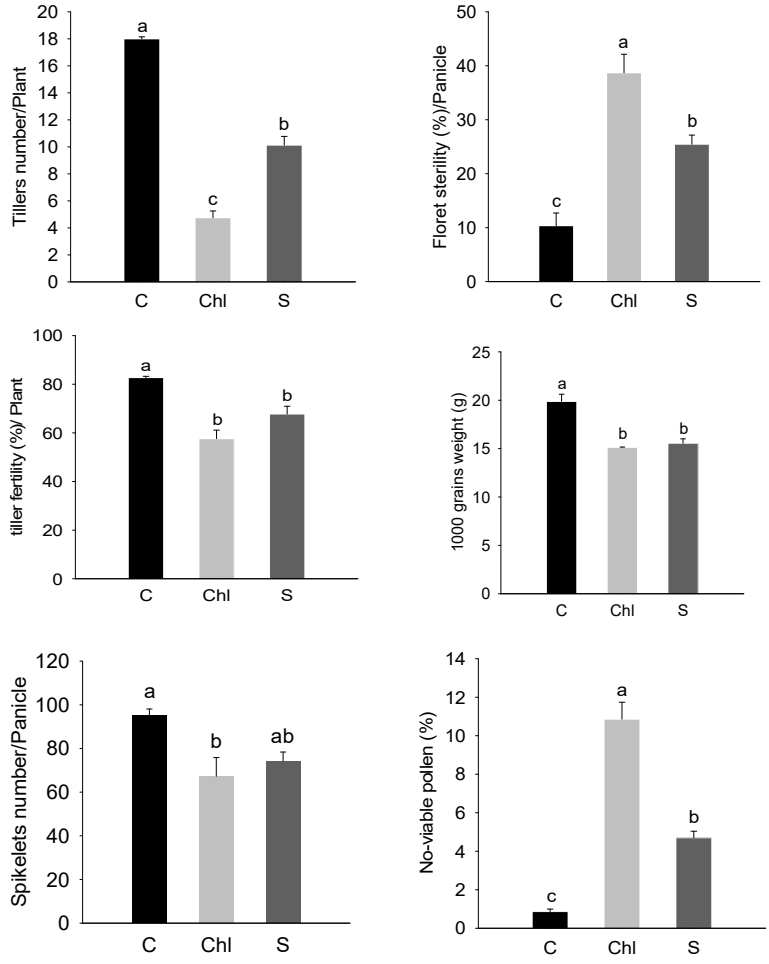

Figure 4. Effects of salinity stress application on vegetative and reproductive growth stages of IKP rice cultivar grown in the Yoshida nutrient solution without salt stress (C), with 40 mM NaCl (Chl) or 20 mM Na_2SO_4 (S). Means with similar letters are not different at $p < 0.05$, according to Tukey's multiple range test at 95%.

For all analyzed elements, the mineral content was higher in the hulls than in the grain itself (Table 2). In both organs, Na^+ accumulation was lower in Na_2SO_4 than in NaCl-treated plants. Treatments had no significant impact on the relative Na^+ distribution and a mean percentage of 91.4% of total Na^+ was accumulated in the hulls. Both types of salinity reduced K^+ content: there was no significant difference between NaCl and Na_2SO_4 in this respect, and salinities had no impact on the relative distribution between hulls and grains. Almost all recorded chloride (more than 95%) was found in the hulls. Chloride concentration increased by 730% in the hulls and by 960% in the grains of NaCl-treated plants, compared to the control. Sulfate salinity had no significant impact on Cl^- content, but increased sulfur content to a higher extent in the hull (583%) than in the grain (152%).

Table 2. Mineral nutrient concentration measured in the grain and grain hull (lemma and palea) of IKP rice cultivar grown in the Yoshida nutrient solution without salt stress (C), with 40 mM NaCl (Chl) or 20 mM Na_2SO_4 (S).

	µmol g^{-1} DW					
	Grain Hull			**Grain**		
Ion	**C**	**Chl**	**S**	**C**	**Chl**	**S**
Na^+	42.8 ± 3.5 ^{c}	503.4 ± 3.2 ^{a}	314 ± 36.5 ^{b}	5.4 ± 0.06 ^{c}	51.7 ± 2.3 ^{a}	22.9 ± 3.5 ^{b}
K^+	920 ± 30 ^{a}	534.9 ± 15 ^{b}	550 ± 24 ^{b}	226 ± 1.5 ^{a}	141 ± 3.6 ^{b}	146 ± 7 ^{b}
Cl^-	199.3 ± 13 ^{b}	1455.6 ± 27 ^{a}	188 ± 14 ^{b}	6.7 ± 0.08 ^{b}	64.6 ± 3 ^{a}	7 ± 0.7 ^{b}
S^{6+}	48.7 ± 5.6 ^{b}	57.2 ± 4.3 ^{b}	284 ± 17 ^{a}	16.4 ± 1 ^{b}	15 ± 0.1 ^{b}	25 ± 2 ^{a}

Means with similar letters are not different at $p < 0.05$ according to Tukey's multiple range test at 95%.

4. Discussion

The present study confirms that flowering-related parameters are especially sensitive to salinity in rice, but it also underlines that the type of salinity (chloride versus sulfate salinities) influences the plant response and that chloride salt was, on the whole, more toxic than sulfate salt. Some studies previously compared salinity and alkalinity impact on the reproductive structure in rice [10,30] but, to the best of our knowledge, data regarding the comparison between NaCl and Na_2SO_4 remain devoted to the vegetative phase of development [23,25,31–34].

Most studies dealing with salt stress focus on Na^+ accumulation, and pay only little attention to the accompanying anion. In order to unravel the putative influence of the counter-anion, we used similar final Na^+ doses in the nutrient solution [35], and the chosen dose induced a low salinity level (4.30 dS.m^{-1}), which is relevant to the salinity occurring in real field conditions. This salinity level was sufficient to inhibit photosynthesis at vegetative stage, and to induce floret sterility at the flowering stage in relation to a decrease in pollen viability, leading to a reduced number of filled grains per panicle.

In addition to the stress intensity, the phenological stage of stress imposition and the duration of the stress also have an influence on flowering parameters. Some studies aiming to specifically analyze the salt effect at the flowering stage apply stress at late-bootting or at the heading stage and, for this purpose, use high salt concentration [36–38]. They provide precious information on the genetic basis of salt-tolerance at the flowering stage, but these studies do not consider the earlier step of inflorescence initiation, although the number of spikelets per panicle and the panicle length are important parameters influencing the final yield in salt-treated rice [7,13].

Long-term exposure to field-relevant levels of salinity also frequently induces a delay in flowering [3]. Such a delay was not observed in the present study since both control and stressed plants simultaneously flowered. Flowering time under salt stress is genetically controlled in cereal plants [39], and it could not be excluded that IKP remains poorly affected in this respect. Parket al. [40] reported that the GIGANTEA protein (GI), encoded by a single gene and involved in the elicitation of photoperiod-dependent flowering, may be degraded in the presence of salt, thus retarding the progression towards flowering; since IKP is a non-photoperiodic cultivar, it may be hypothesized that GI is not necessarily assuming such a crucial role in the control of flowering in this cultivar.

A salt-induced decrease in pollen viability is an important component of stress impact on flowering. According to Khatun and Flowers [22], NaCl reduced pollen staining and viability estimated by tetrazolium salt. According to these authors, Na^+ and Cl^- per se are responsible for poor pollen viability, which also appear during pollen germination in vitro. Some authors, however, observed that in salt-treated plants, the anther tapetum retained most of the toxic ions, and that the poor viability of the pollen should be ascribed to an impact on pollen maturation as a result of an alteration in tapetum metabolism, rather than to a direct accumulation of toxic ions within pollen grains [41]. It is notable, however, that in the present case, NaCl was far more detrimental to pollen viability than

Na_2SO_4. Since the ion content was not estimated in pollen, it is not possible to ascribe pollen viability decrease to ion accumulation. At the whole grain level, Na^+ accumulation was higher in $NaCl^-$ than in Na_2SO_4-treated pants, but these observations valid for grain at the end of the maturation period do not constitute a direct proof that Na^+ previously accumulated to a higher extent in pollen grain. Some authors also mentioned that Cl^- efflux is a crucial component for pollen tube growth [42]. It could therefore be hypothesized that a modification in Cl^- content occurring as a result of NaCl exposure but not in response to Na_2SO_4 may be deleterious for pollen viability. It has also to be mentioned that the difference between the two salt treatments for pollen viability was estimated to be around 8%, while the difference for global florets fertility was higher than 15%, thus suggesting that other components may be responsible for flower sterility. Khatun and Flowers [22] reported that salinity may also induce alteration of stigma receptivity, and the additional localization of ions in the various flower organs should allow us to gain more information on the underlying causes of salt-induced flower sterility. In addition to the ionic component, the osmotic component of salt stress may also have a deleterious impact on flowering and yield-related parameters [19], although this could hardly explain recorded differences between NaCl and Na_2SO_4, which are used in concentrations inducing comparable (although not similar) osmotic potentials in the nutrient solution.

Salinity induced a strong decrease in photosynthesis at both the vegetative and the flowering stage. The recorded decrease in A_N appeared similar for $NaCl^-$ and Na_2SO_4-treated plants, and a salt-induced inhibition of photosynthesis is commonly attributed to stomatal and to non-stomatal causes [5]. At the seedling stage, NaCl and Na_2SO_4 had different impact on stomatal conductance, suggesting that the recorded decrease in A_N observed at this stage may be due to non-stomatal causes. According to Sultana et al. [11], a reduction of photosynthesis in salt-treated rice depends not only on a reduction of available CO_2 by stomatal closure, but also on the cumulative effect of biochemical constituents, such as photosynthetic pigments, soluble carbohydrate and protein. This results in a low concentration of assimilates in the leaves, and poor translocation of assimilates from the source organs reduces grain growth, which is especially sensitive at the milking stage. At the vegetative stage, all photosynthetic pigments were more sensitive to NaCl than to Na_2SO_4, and this could be related to the fact that in IKP, Na^+ accumulation was shown to be higher in the former than in the latter case [25].

In salt-tolerant rice cultivars, Na^+ may frequently accumulate in older leaves to preserve photosynthetic activities of the youngest ones but in salt-sensitive cultivars such as IKP, Na^+ was more evenly distributed among leaves of different ages [4,8,18], and flag leaf appears as the major site of sugar production for grain filling. Imaizumi et al. [43] demonstrated, however, that the leaves (mainly flag leaves) are not the only contributor to grain filling. According to these authors, rice panicle itself (rachis-branches and spikelets) exhibit a photosynthetic activity contributing to grain filling and especially spikelets have a high photosynthetic capability, which is similar to that of the flag leaf. In the present work, we demonstrated that majority of the translocated Na^+, Cl^- and S^{6+} present in the spikelets accumulated in the hulls. If spikelet photosynthesis contributes to grain filling, an important part of the assimilates should be produced in the hulls. Ion accumulation at this level may be explained by the fact that these floral organs exhibit a xylem connection, while phloem is involved in ion translocation to the endosperm. The hulls also present a high density of stomata, which contributes to transpiration and allows CO_2 fixation. Our data provided clear evidence that in NaCl-treated plants, more than 90% of the translocated Na^+ was accumulated in the hulls, and the proportion was even higher for Cl^-. A similar observation is valid for Na^+ and S^{6+} in Na_2SO_4-treated plants. Such a high concentration of ion may impact spikelet photosynthesis, and at least contribute to the decrease in grain weight. Hull may serve as a sink protecting young embryo and maturing endosperm from accumulation of toxic ions, as previously demonstrated for arsenic [44]. However, when the ratio of concentration hull/grain is calculated for Na^+ and Cl^-, no significant differences were observed for Na^+ between the control and stressed plants (ratio from 8.0 to 14.9), as well as for Cl^- (ratio of 29.8 in control and 28 in stressed plants), suggesting that processes operating in sodium and chloride concentration in the hulls are already operating in unstressed plants.

The negative impacts of salinity on the flag leaf photosynthesis, the number of spikelets per panicle and mean 1000-grain weight were similar for NaCl and Na_2SO_4. Although the number of spikelets per panicle decreased in salt-treated plants, salt impact on flag leaf photosynthesis was by far higher, and the decrease in the number of sink organs could, thus, not compensate for photosynthesis inhibition. According to Abdullah et al. [9] starch synthase activity (α 1-4-glucan glucosyl transferase) in developing grain is inhibited by salinity, and this could partly explain the salt-induced decrease in the mean 1000-grain weight. Moderate to high salinities may reduce amylose content and induce numerous functional changes in relation to pasting properties and gel consistency. Thitisaksakul et al. [38] interestingly reported that the salt-induced modification of enzyme activities during the grain filling is a function of timing, and that the recorded effects were not the same for plants exposed to salinity since the seedling stage or since anthesis. According to this study, rice exposed for long period to low level of salt may even show adaptative responses to prolonged salt treatment, and compensate for a decrease in seed fertility by an increase in protein content.

5. Conclusions

In conclusion, NaCl appeared more toxic than Na_2SO_4 for numerous recorded photosynthetic parameters and yield components. In addition to the salinity stress type, the plant stage and the stress duration also showed an influence on photosynthetic and flowering parameters. Salt-induced yield decrease in rice could be attributed to both an inhibition of photosynthesis in leaves, leading to a reduced translocation of assimilates toward the grain, and to a deleterious impact of salinity on the number and the efficiency of reproductive structures.

Author Contributions: S.L., G.R. and W.I. conceived the experiment; S.L. and G.R. supervised the work; W.I. performed the experimental work; S.N. and H.P. contribute to the interpretation of the data; H.P. and W.I. performed the statistical analysis; S.L. and W.I.: writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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