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ARTICLE

The Effect of Water and Salt Stress on *Paspalum dilatatum*, a Constituent of Pampas Natural Grasslands

Claudia A. Porcelli[1], Gerardo Rubio[2], Flavio H. Gutiérrez Boem[2] and Raul S. Lavado[2,*]

[1]Departamento de Química, Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, C1417DSE, Argentina

[2]Instituto de Investigaciones en Biociencias Agricolas y Ambientales (INBA), Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, C1417DSE, Argentina

[*]Corresponding Author: Raul S. Lavado. Email: lavado@agro.uba.ar

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ABSTRACT

The effects of the salt stress on plant growth are usually increased by the water stress. We studied the impact of both stresses in simultaneous pulses of drought and salinity on *Paspalum dilatatum*. This forage species is native to South America, spread in grasslands in many tropical, subtropical, and temperate areas of the world, and very common in grasslands of the Flooding Pampas of Argentina. Mimicking what happens in nature. We compared a pot experiment, a non-stressed control against water stress for a month (midpoint between field capacity and wilting point), and two saline stresses (moderate, 6 $d{\cdot}Sm^{-1}$ and strong, 12 $d{\cdot}Sm^{-1}$), also for a month. Aerial biomass (green leaf; non-leaf green material, and dry material) and roots were harvested, weighed, and analyzed for nitrogen, phosphorus, and cations. The biomass of all components significantly decreased when both stresses were applied. Water plus strong saline stress reduced by half the total biomasses, compared to the control. The proportion of aerial biomass/root biomass ratio as well as aerial green component/dry materials ratio tend to decrease when subjected to both stresses. Nitrogen concentration in plants was not significantly affected, but phosphorus concentration increased in aerial biomass components, from 0.10 to 0.18 $mg{\cdot}kg^{-1}$ between the extreme treatments, but did not change in roots. Sodium concentration in plants increased (i.e., in green leave sodium (Na) increased from 0.27 to 2.01 $mg{\cdot}kg^{-1}$ between the extreme treatments), whereas other cations either did not change or decreased, affecting the ratios between them. Sodium performance allows us to infer that the Na accumulation of *P. dilatatum* behaves in an intermediate range, compared to very tolerant to salts or non-salt tolerant species of the *Paspalum* genus. In agreement, when salts were applied in the form of a pulse, *P. dilatatum* tolerated higher salinity than that found by other authors for the same species, using continuous salinity.

KEYWORDS

Dallis grass; salinity; drought; sodium in plants; phosphorus in plants; potassium/sodium ratio

Nomenclature

AOAC	Association of Official Agricultural Chemists
ANOVA	Analysis of Variance
EC	Electrical Conductivity
FAO	Food and Agriculture Organization
FC	Field Capacity

RWC	Relative Water Content
SS	Salinity Stress
WP	Permanent Wilting Point
WS	Water Stress

1 Introduction

Paspalum dilatatum, known as Dallis grass, is a C4 forage grass native to South America. Although this species is spread all over the tropical, subtropical, and temperate areas of the world [1,2], it is a vigorous, persistent, and highly palatable species that withstands heavy grazing. This species is conspicuous or even co-dominant in most plant communities of the Flooding Pampas (Argentina). Different than other subregions of the Pampas, the Flooding Pampas remain covered mainly by temperate native grasslands, mainly due to the simultaneous occurrence of water and salt stress [3]. The area is characterized as a wet one, suffering commonly water logging conditions in winter and early spring, and even flooding, while soils show a low salt concentration. However, water and salt stresses are concurrent during most summers when drought occurs together with sudden increases in topsoil salinity. After late autumn rainfalls, water stress diminishes and salinity returns to its low current level, showing clearly the temporal variation of salinity in nature [3].

Water and salt stress impose an adverse impact on plant biomass production. They are usually related. Water stress has been identified as the single most biomass-reducing factor for the plants [4,5]. It is an almost universal plant stress, either permanent or transient, and periods of drought may occur frequently, even in regions characterized by high annual rainfall [4]. The present global warming situation increased drought occurrence around the globe [4]. Drought conditions affect the growth of plants by affecting photosynthetic and biochemical processes which result in a substantial decline in crop productivity [4,6]. Salt stress is usually localized from arid to humid areas, salt stress has a profound effect on both natural vegetation and crops, in certain conditions, salt stress may resemble water stress. Salts cause osmotic or water-deficit effects, in addition to salt-specific effects. The water deficit mediated by salts occurs because the presence of salts reduces the water uptake of plants which leads to a decrease in growth rate, accompanied by various metabolic changes similar to those induced by water stress [7]. The specific effects of salts are attributed to the intake of excess Na^+ and Cl^- ions [4,8]. Recent studies have revealed that the response of plants to a combination of water and salt stresses is unique and cannot be directly extrapolated from the response of plants to each of the different stresses applied individually [9,10].

Water and salt stresses can differentially affect the mineral nutrition of plants by reducing nutrient uptake by the roots and transport from the roots to the shoots, by restricting transpiration rates and impairing active transport, and membrane permeability [7,10]. Salinity stress also induces nutrient deficiency or causes nutrient imbalance due to the competition among them, such as potassium (K), calcium (Ca), and sodium (Na) [11]. Several studies have shown that *P. dilatatum* is tolerant of both floods and drought [12–14]. Cook et al. [15] indicated that this species is remarkably tolerant of drought because of its thick rhizomes. On the other hand, from the pioneering work of Gauch et al. [16] *P. dilatatum* is known as a species moderately resistant to salinity [17,18]; According to Lair [18], upper limits of this species survival is around 8–12 $d{\cdot}Sm^{-1}$. Other species of the genera, like *Paspalum vaginatum* Swartz, are highly tolerant to salts [19,20]. According to Chavarria et al. [21], *Paspalum vaginatum* reduces its performance by 62% on average, at Electrical conductivity (EC) as high as 45 $d{\cdot}Sm^{-1}$. It is remarkable that *Paspalum vaginatum* is also found in the Flooding Pampas grasslands, but is much less conspicuous than *P. dilatatum* [8]. While most studies were performed using a continuous salt supply, crops respond differently when coping with continuous salinity *vs.* peaks or pulses of salts [11].

Our objective was to determine the effects of drought and salinity on biomass production of the green and dry components and chemical composition of *Paspalum dilatatum* plantlets, mimicking the stress conditions in the form of pulses of water deficit and salt excess. We hypothesize that the simultaneous negative effect of water stress and salt stress on the biomass production of *P. dilatatum* increases with the magnitude of salt stress.

2 Materials and Methods

2.1 Soil and Plants

A pot experiment was carried out at a rainout shelter on the campus of the School of Agriculture, University of Buenos Aires, Buenos Aires, Argentina (34°36′S, 58°29′W). The pots were filled with 3 kg of the A horizon of a General Guido series Typic Natraquoll, collected near the town of Casalins (Buenos Aires Province). The soil is representative of the sodic soils widespread in the Flooding Pampas. The analysis of the A horizon samples was carried out using standard soil test methods. The analysis of the A horizon samples was carried out using standard soil test methods [22] for the physical and chemical properties: Particle size distribution (Pipette method) was 18.0% clay, 33.9% silt, and 48.1% sand, indicating a Loam texture; Water retention at Field Capacity (33 kPa) was 21.8% and at Permanent Wilting Point (1500 kPa) 11.0%; total carbon (Walkley and Black method) was 18.5 $g \cdot kg^{-1}$, pH was 7.0, available P (Kurtz and Bray method) was 12.5 $mg \cdot Kg^{-1}$ and EC was 0.5 $d \cdot Sm^{-1}$. *Paspalum dilatatum* plantlets were taken from the grassland community growing on that soil. The temperature in the shelter varied from a daily minimum of 13°C to 19°C to a maximum of 32°C to 42°C. Water was provided via irrigation.

2.2 Experimental

We adopted a completely randomized design with 4 replicates of a factorial arrangement of two factors: two levels of water stress (WS) and three levels of salinity stress (SS). There were 6 treatments: Control, SS0/WS0 (natural soil with adequate water supply); Water stress, SS0/WS1; Moderately saline stress, SS1/WS0; water stress plus moderately saline stress SS1/WS1; Strong saline stress, SS2/WS0 and Water stress plus strong saline stress, SS2/WS1. Both saline and water stress were applied during the same time period. The water status was controlled by irrigation with distilled water, adding the water from the top. The pots of the Control (SS0/WS0) were maintained near field capacity during the course of the experiment, allowing the water to drain (Fig. A1). All pots have drainage holes in the bottom. The pots of the treatments with water stress were maintained equally around field capacity, from the start of the experiment on late spring. Subsequently, they were maintained in the middle point between field capacity and wilting point for a month (i.e., January) by weighing the pots on a daily basis and avoiding drainage. By early February the pots were irrigated again as indicated previously to reach field capacity. The salt stress treatments were irrigated initially with distilled water and in January both salt stress treatments were carried out by irrigation with saline solutions of two different EC: for the moderate salt level, 6 dSm^1 and for the strong salt level, 12 dSm^1. The saline stress treatments were obtained dissolving the quantity of sodium chloride in distilled water to obtain the desired EC. The salt concentration in the pots was maintained in all treatments allowing solution percolation, because in such a way the soil solution equals the percolating solution. For the treatments subjected simultaneously to both stresses, at that point, the addition of each salt solution was stopped and water was applied as indicated for water stress treatment, by weighing the pots. At the end of the thirty days period, distilled water was applied in excess to reduce salinity, making use of drainage holes in the bottom of the pots. The surplus of water (20% more than needed to maintain field capacity) flushed the salt out in few days, which was assured by checking the EC of percolates (data not shown). The pots were irrigated again to field capacity using distilled water, until the end of the experiment.

2.3 Harvest and Analysis

In March the experiment ended and the aerial biomass and roots were collected in all pots. The aerial biomass was divided into green leaves; non-leaf green material (shoots, inflorescences, etc.) and dry material (dry leaves, dry shoots, etc.). Roots were removed from the soil. All this material was dried at 70°C and weighed. The chemical determinations were carried out using standard techniques: nitrogen (N) (Kjeldhal method), phosphorus (P) (extracted by calcination and dissolution of the ashes, and determined by the Murphy and Riley colorimetric methodology), and Ca, Mg, K and Na digested in hot $HClO_4$ and HNO_3 and determined by atomic absorption spectrophotometer [22,23]. Previously, in January, when stress treatments were ending, Relative Water Content (RWC) was determined by oven drying at 80°C for 24 h samples of fresh, turgid green leaves [24].

2.4 Statistics

The data of aerial biomass, root biomass N and P in aerial and root biomass and foliar Na, K, Ca and Mg were statistically analyzed using the RStudio software (version 1.1.453 for Windows RStudio Team 2015) for an ANOVA analysis, after testing the variables for normality and homogeneity of variance. When there was a significant effect of the treatment, contrasts (Student's *t*-test) were used to compare the means.

3 Results

The effects of the different treatments on total aerial biomass and its components and on root biomass are shown in Fig. 1 and in Table 1.

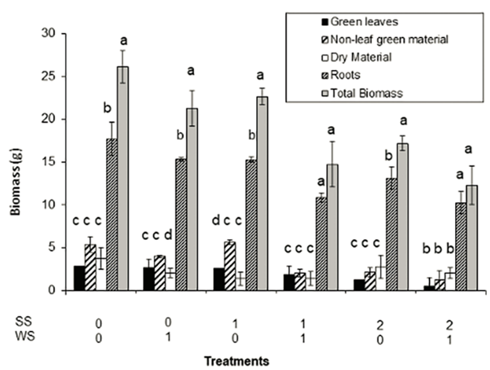

Figure 1: Biomass production of *Paspalum dilatatum* discriminated in green leaves, non-leaf green material (shoots, inflorescences, etc.), dry material (dry leaves, dry shoots, etc.) and roots, as influenced by the two factors studied (WS, SS). Bars represent standard deviation. Different letters mean significant differences

Table 1: Significance levels (*p* values) of factorial ANOVAs of the measured plant parameters

Factors	Aerial biomass	Root biomass	Nutrient concentration						
			N (aerial and roots)	P Aerial	P roots	Na total	K total	Ca total	Mg total
Water stress (WS)	<0.001	<0.001	Ns	<0.01	ns	<0.001	ns	Ns	ns
Salt stress (SS)	<0.001	<0.001	Ns	<0.01	ns	<0.001	ns	Ns	ns
WS × SS	<0.001	0.01	Ns	<0.001	ns	<0.001	ns	Ns	ns

Fig. 1 shows that all plant components significantly decreased when subjected to both stresses while Table 2 shows the statistical significance of the found results. The extreme stress treatment (SS2/WS1) reduced to a half total biomass when compared to control. In all cases the whole aerial biomass was lower than the root biomass: the aerial biomass varied from 67% compared to root biomass in the check treatment to 37% in the treatment SS2/WS1.The proportion of dry rest to green components of the plants was also affected by the treatments. In all cases but in one, the dry materials were lower, from 18% to 83%, than the green components. The exception was treatment subjected to both water plus strong saline stress (SS2/WS1), in which the green components account 88% of the dry rest. Using the RWC as an indicator of water deficit, the significant effects of water and salt stress were verified on *P. dilatatum* ($p <$ 0.001 and $p < 0.02$, respectively) (Fig. 2).

Table 2: Calcium, magnesium, sodium and potassium concentrations ($mg \cdot kg^{-1}$) in green leaves, non-leaf green material, dry material (dry leaves, dry shoots, etc.) and roots of *Paspalum dilatatum*), as influence by the two studied factors (water stress and salinity stress). Italicized numbers are the standard deviation (N = 4). Different letters mean significant differences

Treatment		Green leaves				Non-leaf green material				Dry material				Roots			
SS	WS	Ca	Mg	Na	K	Ca	Mg	Na	K	Ca	Mg	Na	K	Ca	Mg	Na	K
0	0	0.40	0.22	0.27	2.36	0.31	0.18	0.22	2.25	0.43	0.36	0.32	1.90	0.50	0.16	0.85	0.34
		0.02	0.03	0.14	0.63	0.05	0.03	0.05	0.52	0.04	0.02	0.25	0.11	0.02	0.25	0.11	0.01
0	1	0.39	0.22	0.24	2.46	0.25	0.20	0.37	2.00	0.41	0.30	0.39	1.99	0.46	0.14	0.99	0.34
		0.05	0.03	0.13	0.42	0.02	0.01	0.15	0.11	0.03	0.02	0.18.	0.05	0.02	0.18	0.05	0.01
1	0	0.47	0.24	0.65a	2.87	0.30	0.23	0.83d	2.39	0.41	0.40	0.88c	2.13	0.46	0.14	1.12c	0.32
		0.04	0.05	0.10	0.27	0.03	0.03	0.23	0.35	0.04	0.01	0.44	0.07	0.01	0.44	0.07	0.00
1	1	0.50	0.27	1.59a	2.96	0.35	0.26	1.27	2.22	0.40	0.36	1.06c	2.40	0,49	0.14	1.28c	0.32
		0.03	0.02	0.28	0.42	0.03	0.03	0.28	0.17	0.04	0.01	0.31	0.04	0.01	0.31	0.04	0.01
2	0	0.48	0.20	1.62a	2.58	0.36	0.26	1.80b	1.79	0.43	0.35	1.84b	2.17	0.50	0.15	1.59b	0.24
		0.04	0.03	0.34	0.42	0.03	0.03	0.23	0.48	0.01	0.01	0.41	0.07	0.01	0.41	0.07	0.01
2	1	0.39	0.14	2.01a	2.68	0.39	0.26	2.58a	2.13	0.43	0.32	2.23a	2.40	0.57	0.15	1.81a	0.22
		0.04	0.56	1.63	0.89	0.07	0.02	0.91	0.41	0.05	0.01	0.53	0.05	0.01	0.53	0.05	0.01

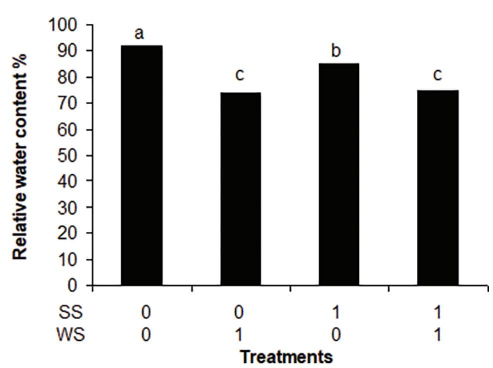

Figure 2: Influence of water and saline stress on relative water content in *Paspalum dilatatum* leaves, measured through the relative water content in green leaves. Different letters mean significant differences

Sodium, K, Ca and Mg concentration in plant components are shown in Table 2.

The N concentration in the different components of the plants showed no significant differences due to the imposed treatments. The green leaves and non-leaf green material contained to 0.85–1.39 mg N·kg^{-1}, dry material to 0.21–0.60 mg N·kg^{-1} and roots to 0.81–1.10 mg N·kg^{-1}. P concentration increased significantly in green leaves, non-leaf green material and dry material, as stress, especially salinity, increased. Conversely, P concentration in roots did not show significant differences in any of the treatments (Fig. 3).

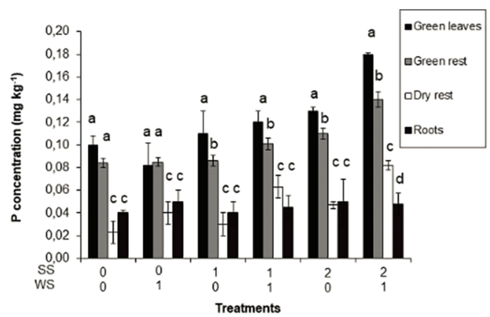

Figure 3: Phosphorus concentration in green leaves, green rest (non-leaf green material—shoots, inflorescences, etc.), dry rest (dry material—dry leaves, dry shoots, etc.) and roots of *Paspalum dilatatum*, as influenced by the two factors studied (water stress and salinity stress). Bars represent standard deviation. Different letters mean significant differences

Potassium, Ca and Mg concentrations were not largely affected by the imposed treatments in green leaves, non-leaf green material and dry material, as compared with control (Table 2). Conversely, Na concentration increased significantly in these plant components as salinity stress increased. (Table 2). Consequently, the K/Na ratio in all aerial plant components (Fig. 4) as well as the Ca/Na (Fig. 5) and Mg/Na ratios (data not shown) decreased ($p < 0.001$). Sodium concentration did not increase in roots and as a consequent the Na/K and Ca/Mg ratios in roots were not affected by the treatments.

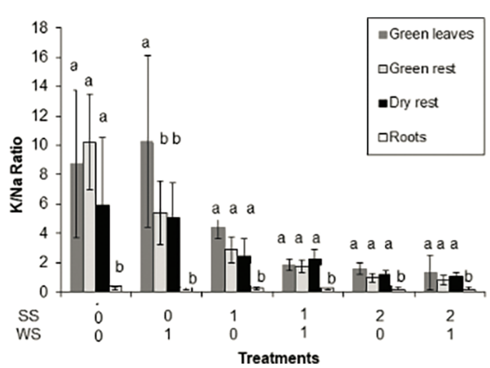

Figure 4: K/Na ratio in green leaves, green rest (non-leaf green material—shoots, inflorescences, etc.), dry rest (dry material—dry leaves, dry shoots, etc.) and roots of *Paspalum dilatatum*, as influenced by the two factors studied, water stress and salinity stress (WS, SS). Bars represent standard deviation. Different letters mean significant differences

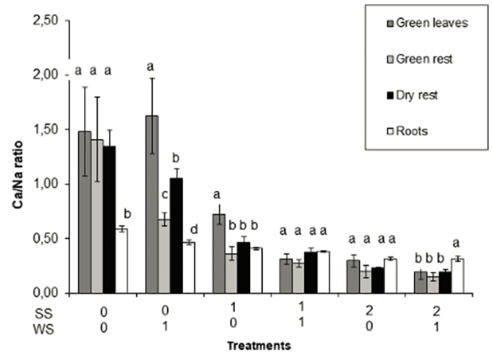

Figure 5: Ca/Na ratio in green leaves, green rest (non-leaf green material—shoots, inflorescences, etc.), dry rest (dry material—dry leaves, dry shoots, etc.) and roots of *Paspalum dilatatum*, as influenced by the two factors studied, water stress and salinity (WS, SS). Bars represent standard deviation. Different letters mean significant differences

4 Discussion

The effects of water stress on plants depend on its absolute value and temporal variation [25]. In present case plant components significantly decreased when subjected to both stresses, but different than reported [5] the whole aerial biomass was more affected than the root biomass.

In the present experiment the RWC measured at the end of the stress period corresponded to a level equivalent to initial wilting stage [19]. The RWC was more critical on salt stressed treatments, which agree with the fresh/dry weight ratio which diminishes under water limitation [19]. These results are similar to that found by Lee et al. [20] with different ecotypes of the salt tolerant *Paspalum vaginatum*, although when subjected to a salinity increase. results varied among ecotypes. The RWC decreased under water stress although somewhat less than with salt stress, in agreement with the moderately tolerance to drought of *P. dilatatum* [5,15]. Focusing on salt stress effects, the results show that *P. dilatatum* subjected to salt pulses, even including water stress, can tolerate more salinity than is shown by classical experiments using continuous salinity regime and without water stress [16–18]. Water stress is normally a coexisting factor with salt stress, however, the effect of the superposition of both on *P. dilatatum* cannot be quantified in this work. Anyway, different results show that due to plants subjected to pulses of salinity accumulate fewer ions in their tissues they can tolerate higher salinities than those subjected to continuous salinity [11].

Results showing that leaf N concentration did not vary due to the imposed treatments, but P concentration increased significantly confirm that the interactions between N and P nutrition and water and salt stress are complex. It depends on the magnitude of the stress and the stress tolerance of plants [26]. Yadav et al. [8] indicated that the water stress results in N absorption limitations. Salt stress (as well as other stresses) may reduce N accumulation [7,26] but in our experiment, the plant N concentrations were not affected by the treatments. The N concentration in green leaves was similar than that obtained previously in *P. dilatatum* from the Flooding Pampas by Ayala Torales et al. [27] and Vivanco et al. [28]. However, our foliar N concentration was lower than that found by Andrew et al. [29] in other latitudes and also lower than that recorded for *Paspalum vaginatum* [19]. The saline stress may decrease, increase or not affect P accumulation in plants [7,26]. In our case, the P concentration in plant tissues increased with the treatments but, this fact could be related to lower biomass production, as usually established: the lower the biomass, the higher the P concentration [30]. Phosphorus concentration in leaves was similar as those obtained by Vivanco et al. [28] and again lower than those found by Andrew et al. [29].

In general terms non-halophytic plants tend to absorb Na in excess in saline soils, causing a relative and even absolute decrease in K and Ca concentration. These processes are related to the K-Na antagonism [26]. The Ca/Na ratio, which is related to plant salt tolerance, is also affected [8,31]. In the present case, the Na concentration increased, except in the roots, while that of the rest of the cations was not substantially modified (Table 2), which caused the K/Na, Ca/Na and Mg/Na ratios to decrease in all components. aerials (Figs. 4 and 5). The highly salt tolerant *Paspalum vaginatum* can maintain a high concentration of K in its shoots and can limit the movement of Na toward shoots. Besides, this species accumulated more Na and Ca in its dead leaves than in the green leaves. The maintenance of a high K/Na ratio allow *P. vaginatum* to avoid the cation damage caused by salt stress [19], different than the non-salt tolerant *P. scrobiculatum*, which is unable to regulate the transfer of Na from the green leaves [32].

This suggested that one way by which *P. vaginatum* tolerates salinity may be by a mechanism of reducing Na transport to leaves and moving excess of cations from young leaves to older and possibly dying leaves [32]. In our experiments, the combined effects of water and salt stress on cationic concentrations was complex because there were large differences in its concentration between the different plant components. Most results in present experiment (Table 2) showed that *P. dilatatum* when subjected to salinity stress did not show the same behavior than the salt tolerant *P. vaginatum*, with which coexist in the grasslands. Different from that species, our results show that *P. dilatatum* does not accumulate Na and Ca in dead leaves.

We found that the representation of natural conditions in a controlled experiment provides some different results as compared with similar experiments but where is not considered the variability of salinity and the water stress. The comparison with other species of the same genus allowed us to advance with the way this species deals with salinity, but this is a further field to study. From a more applied point of view, the present data contribute to better knowledge of the species for a more rational management of natural grasslands.

5 Conclusion

P. dilatatum biomass production in the different plant components, green leaves, non-leaf green material, dry material, and roots, decreased when subjected to individual stress and decreased even more when both stresses were applied simultaneously. However, under the conditions of the present experiment, the hypothesis was not validated: the lower and the higher saline stress affected biomass in a globally similar way when subjected to simultaneous water stress. When salts were applied in the form of a pulse, mimicking the nature, *P. dilatatum* tolerated higher salinity than that found by other authors using non-realistic permanent salt levels. Besides this fact, the plant chemical composition related to the accumulation of cations in plant tissues allows us to infer that the Na accumulation of *P. dilatatum* behaves in an intermediate range, compared to salt-tolerant or non-salt tolerant species of the *Paspalum* genus.

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Availability of Data and Materials: Data are available on request from Raul S. Lavado.

Ethics Approval: Not applicable.

Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

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Appendix A

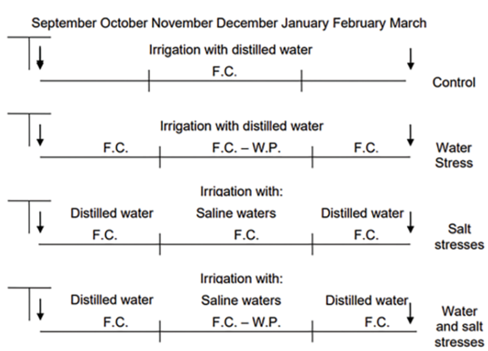

Figure A1: Treatment application scheme