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Salt and Water Stress Tolerance in *Ipomoea purpurea* and *Ipomoea tricolor*, Two Ornamentals with Invasive Potential

Diana-Maria Mircea [1,2], Riwen Li [1], Lorena Blasco Giménez [1], Oscar Vicente [3], Adriana F. Sestras [2], Radu E. Sestras [4], Mónica Boscaiu [1,*] and Ricardo Mir [3]

[1] Mediterranean Agroforestry Institute (IAM), Universitat Politècnica de València, Camino de Vera s/n, 46022 Valencia, Spain; dmircea@doctor.upv.es (D.-M.M.); rli7@posgrado.upv.es (R.L.); loblagi@etsiamn.upv.es (L.B.G.)
[2] Department of Forestry, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, 3-5 Manastur Street, 400372 Cluj-Napoca, Romania; adriana.sestras@usamvcluj.ro
[3] Institute for the Conservation and Improvement of Valencian Agrodiversity (COMAV), Universitat Politècnica de València, Camino de Vera s/n, 46022 Valencia, Spain; ovicente@upvnet.upv.es (O.V.); rimimo@upvnet.upv.es (R.M.)
[4] Department of Horticulture and Landscape, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, 3-5 Manastur Street, 400372 Cluj-Napoca, Romania; rsestras@usamvcluj.ro
* Correspondence: mobosnea@eaf.upv.es

Abstract: Invasive plants pose a significant threat to biodiversity, especially under the current unstable climatic conditions. This study aimed to test the salt and drought tolerance of two ornamental species of the genus *Ipomoea* during germination and vegetative growth. Germination tests were performed in the presence of increasing NaCl concentrations or iso-osmotic PEG concentrations—to mimic the osmotic stress caused by drought. Both species showed great invasive potential because of their high seed germination percentages and rapid germination under control (distilled water) and salt stress conditions, up to 200 mM NaCl. Germination and early seedling development were more affected in the presence of PEG. Subsequently, water stress (complete withholding of irrigation) and salt stress (watering with 100 mM and 200 mM NaCl) treatments were applied to young plants for three weeks, when all plants were harvested, to determine several morphological and biochemical parameters. Both species were sensitive to water deficit but relatively resistant to salt stress. Their salt stress responses were similar, based mainly on the inhibition of Na^+ and the activation of K^+ transport from roots to leaves and the uptake and accumulation of Ca^{2+}; however, *I. tricolor* showed a slightly higher tolerance to salt stress than *I. purpurea*. Although *I. tricolor* has only been locally reported as invasive and is generally considered a 'low-risk' species, our results indicate that it may have an invasive potential even higher than *I. purpurea*, a recognised invasive weed, spread into areas with moderate salinity, affecting agricultural land or natural habitats of ecological interest.

Keywords: ornamental plants; invasive potential; seed germination; vegetative growth; photosynthetic pigments; compatible solutes; ion concentrations

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1. Introduction

One of the most significant risks for biodiversity on a global scale is represented by the spread of invasive species, which is exacerbated by globalisation and climate change. They are often the result of intentional or accidental introductions of alien species into new territories, followed by their naturalisation and spread, which provokes a detriment to native species and ecosystems. Invasive species have been recognised for several decades as one of the main threats to endangered plants, exceeded only by habitat loss [1]. At the beginning of this century, 57% of threatened species were reported to be negatively affected by non-native competitors [2]. Invasive alien species compete with native species, alter food webs, nitrogen [3] and hydrological [4] cycles, and thus, disrupt the functioning

of ecosystems and the services they provide [5]. In addition to these ecological effects, invasive species can have a negative economic impact [6] or affect human health [7,8]. The risks posed by invasive alien species are well understood [9,10], as reflected in a growing number of papers and metadata analyses [11–16]. However, the spread and establishment of alien species worldwide is not slowing down [17] and is expected to increase [18] despite prevention measures.

The leading cause of plant invasions is ornamental horticulture, as most invasive alien plants were either actively introduced for ornamental purposes or accidentally, such as seeds brought in by chance [19,20]. The economic importance of plants is a driver of their condition as potential invaders. In this sense, species used for ornamental, medicinal or culinary purposes or for fodder have the highest likelihood of naturalisation [2]. Horticulture might promote plant invasions by selecting species and genotypes of ornamental value based on features that inadvertently encourage spread [20]. Adaptability to the environment, quick germination and profusion of seedling emergence, rapid vegetative development, and early flowering or prolonged flowering periods are all characteristics of invasive plants that are also desirable as ornamental plants.

Plant invasions and climate change are closely linked [21]. Europe, the north-eastern United States, Central America, Africa, Indonesia, and Pacific Island regions are considered the areas with the highest susceptibility to invasion by alien species as their climatic conditions could be significantly altered [22]. Increasing temperatures promote the growth of introduced ornamental plants from warmer areas, allowing them to spread into temperate regions [23,24]. Before other species were forced to migrate due to climate change, these invasive species will have a "head start" in the new climatic conditions [25]. Moreover, abiotic stress-tolerant cultivars are preferred for ornamental horticulture in some regions to overcome problems derived from climate change and global warming [23]. Finally, the higher phenotypic plasticity of invasive plants, reported in many comparative studies on invasive and non-invasive taxonomically related species [26,27], favours its spread to new habitats.

With 600–700 species primarily found in tropical and warm temperate regions of the world and known as "morning glories", *Ipomoea* L. is one of the prominent genera within the family *Convolvulaceae*. Most species in this genus are climbers, annual or perennial herbaceous plants, and shrubs [28]. The genus includes *I. batatas* (L.) Lam, the sweet potato, originated in America and is cultivated throughout the world where the climate conditions allow its growth [29], as well as many other species used for ornamental purposes due to the outstanding appearance of their flowers and their climbing habit, which makes them suitable for covering walls, fences, and pergolas. Plants of this genus have rapid growth and high seed production that confers them a high adaptability and microevolutionary capacity, which are typical "weedy traits" [30]. Around 170 species within the *Ipomoea* genus are listed in the Global Compendium of Weeds, and many are reported as invasive worldwide [31]. Two species of this genus, *I. purpurea* (L.) Roth and *I. tricolor* Cav. were selected for this study. The two are popular in temperate and warm regions of the world as cover plants for walls, fences and pergolas due to their large, showy flowers of beautiful colours, white to pink, blue and dark purple. Both have abundant seed production and fast growth, traits that favour invasiveness. Their ability to withstand abiotic stress has been analysed only in a few studies, and there is virtually no information on their biochemical responses to salinity and drought.

Ipomoea purpurea, the tall morning glory, is an annual vine first reported in England, where it was introduced via Spain from Central America. Nowadays, it is classified as a common weed rated with high global risk in many warm regions, including southern Europe [31,32]. *Ipomoea purpurea* affects different crops, orchards, and nursery production, inducing stunted growth, reduced yields, and hindering harvesting [33]. In warm, humid environments, the species outcompetes native plants, mainly invading riparian forests, wetlands, and coastal areas [32,34]. Once established in natural places, the tall morning glory can spread quickly by climbing on mature trees, shrubs, and other plant species,

generating a dense canopy that competes with the supporting species for nutrients, water, and solar radiation [35,36].

Ipomoea tricolor, the Mexican morning glory, is an annual vine species native to Mexico and cultivated worldwide in mild climates. The species has been long cultivated in Spain and reported as naturalised in the last decades of the 19th century [37] but is generally not problematic as invasive. Although included in the Global Compendium of Weeds [31], it is rated as low risk. It has been reported as a weed for loofah, forage legumes, mango, okra, and sorghum fields in Mexico [38] and recently reported as naturalised in Turkey and predicted to spread to the areas near the Black Sea, Aegean, Mediterranean, and some parts of central Anatolia [39].

This study aimed to unveil the reason for the higher invasive risk of *I. purpurea* over *I. tricolor* by analysing their germination and growth under optimal control conditions and two common environmental stresses, salinity and water scarcity. Osmolyte synthesis and ion accumulation, two main mechanisms of stress responses, were also analysed to better comprehend the differences between the two species. The working hypothesis is that *I. purpurea*, with a higher invasive potential, will show a broader tolerance to stress based on more efficient biochemical responses.

2. Materials and Methods

2.1. Plant Material

Plants were obtained by germinating seeds purchased from Vilmorin Seed Generation, Paris, France.

2.2. Seed Germination

Seeds were placed in standard 90 mm diameter Petri dishes on two disks of filter paper moistened with 2.5 mL of distilled water for the control treatment or with increasing concentrations of NaCl or PEG 6000 (Polyethylene Glycol) for the stress treatments. Controls and treated seeds were covered with two other filter paper disks moistened with the same amount of distilled water or the respective stress treatment solutions. The germination assays were carried out with four replications per treatment and species, with ten seeds in each plate. The salt concentrations tested were 50, 100, 200 and 400 mM NaCl in aqueous solutions, and the corresponding iso-osmotic PEG concentrations ensuring osmotic potentials of −22, −44, −88, and −1.76 MPa, calculated by applying the Van't Hoff equation [40]. Germination was performed in an EQUiTEC germination chamber (LAF Technologies, Bayswater North, VIC, Australia) at 30 °C for 16 h and at 20 °C for 8 h, with a relative humidity of 65%.

The number of germinated seeds was counted every two days for three weeks, considering germination as the emergence of a radicle of at least 2 mm. The germination capacity was expressed as the percentage of germination (GP), and the velocity of germination rate as mean germination time (MGT), calculated according to the formula by Ellis and Roberts [41]:

$$MGT = \sum Dn / \sum n,$$

where D represents the number of days from the beginning of the germination test, and n is the number of seeds newly germinated on day D.

Lengths of the radicle and hypocotyl were measured at the end of the germination assay using Digimizer v.4.6.1 software (MedCalc Software, Ostend, Belgium, 2005–2016).

Other germination indexes calculated were: first germination day (FGD), last germination day (LGD), first day of germination (FDG), last day of germination (LDG), time spread of germination (TSG; differences in time between the last germination day and the first germination day), speed of emergence (SE), and seedling vigour index (SVI), calculated as follows [42]:

$$SVI = (\text{Seedling length, in mm} \times \text{Germination percentage})/100.$$

2.3. Plant Growth and Stress Treatments

The seedlings from the controls in the germination experiments mentioned above were manually transferred into plastic pots (12 cm in diameter) filled with commercial peat (26% organic carbon, pH = 7.0, and EC = 0.6 dS m^{-1}), placed in the greenhouse, and watered twice a week with tap water. Four weeks after transplanting, stress treatments were initiated, using five biological replicas (individual plants) per species and treatment. The pots were placed in plastic trays (10 pots per tray) and watered twice weekly, adding 1.5 L tap water to each tray for the control plants and the same amount of the corresponding NaCl solutions for the salt treatments. The water stress treatment consisted of total irrigation suppression. After three weeks of treatment, when the soil moisture of the water stress group reached 5–8%, plants were harvested, and the aerial part and roots were sampled and processed separately, the latter after being thoroughly cleaned with a brush. The following morphological parameters were registered: root length (RL), stem length (SL), number of leaves (LN), fresh weight of roots (RFW) and leaves (LFW), and water content of roots (RWC) and leaves (LWC). For the calculation of water content (WC), a fraction of the root and leaf material was weighed before (fresh weight, FW) and after drying at 65 °C for 72 h (dry weight, DW), and the following equation was used:

$$WC\% = [(FW - DW)/FW] \times 100 \quad (1)$$

Fresh plant material was frozen in liquid N_2 and stored at −75 °C, and dry material was kept at room temperature in tightly closed bags for further analysis.

2.4. Photosynthetic Pigments

Fresh shoot material (0.05 g) was ground and extracted overnight in ice-cold 80% acetone. The absorbance of the supernatant was then measured at 470 nm, 646 nm and 663 nm. Concentrations of chlorophyll *a* (Chl a), chlorophyll *b* (Chl b) and carotenoids (Caro) were calculated according to Lichtenthaler and Wellburn [43] and expressed in mg g^{-1} DW.

2.5. Ion Content Measurements

The concentrations of sodium (Na^+), potassium (K^+), calcium (Ca^{2+}) and chloride (Cl^-) were determined separately in roots and leaves following the method described by Weimberg [44]. Samples of 0.1 g ground dry material were extracted in boiling Milli-Q water, cooled on ice and filtered through a 0.45 µm Gelman nylon filter (Pall Corporation, Port Washington, NY, USA). The cations were quantified with a PFP7 flame photometer (Jenway Inc., Burlington, VT, USA), and Cl^- was measured using a chlorimeter Sherwood 926 (Cambridge, UK).

2.6. Osmolyte Concentrations

Proline (Pro) concentration was quantified following the classical protocol by Bates et al., as previously described [45]. Fresh ground material (0.05 g) was extracted in 3% (*w*/*v*) aqueous sulphosalicylic acid. Samples were sequentially mixed with acid ninhydrin, incubated in a water bath for 1 h at 95 °C, cooled on ice, and then extracted with toluene. The absorbance of the organic phase was measured at 520 nm, using toluene as the blank. Samples of known Pro concentration were assayed in parallel to obtain a standard curve, and Pro concentrations were expressed as µmol g^{-1} DW.

Total soluble sugars (TSS) were determined following the method of Dubois et al. [46]. Samples of 0.05 g fresh ground material were extracted overnight with 80% (*v*/*v*) methanol, and the supernatant obtained upon centrifugation was mixed with 5% phenol and concentrated sulphuric acid. Spectrophotometric measurements were then performed at 490 nm. TSS concentrations were expressed as equivalents of glucose, used as the standard (mg eq. glucose g^{-1} DW).

2.7. Statistical Analysis

Statgraphics Centurion XVI (Statgraphics Technologies, The Plains, VA, USA) and SPSS Statistics statistical software, version 25.0.0 (IBM SPSS Statistics) were used to analyse the statistical data.

The effects of the stress treatments on the characteristics examined for each species were estimated using a one-way analysis of variance (ANOVA). If the null hypothesis was rejected, the Tukey test was employed as a post-hoc test using a 0.05 *p*-value to analyse the differences. Principal Component Analyses were carried out independently for plant growth and germination, considering the mean values of germination variables and significant biochemical and growth parameters.

3. Results

3.1. Seed Germination

Seeds of both, *I. purpurea* and *I. tricolor*, germinated up to concentrations of 400 mM NaCl, considering germination as radicle emergence. Seeds under PEG treatments showed a lower germination percentage and speed than the isosmotic solutions for both species; under the highest PEG concentration, equivalent to an osmotic potential of −1.76 MPa, no radicle emergence occurred (Figure 1). The pattern of germination evolution over 21 days was similar in the two species under NaCl and PEG treatments (compare Figure 1a,c, and Figure 1b,d).

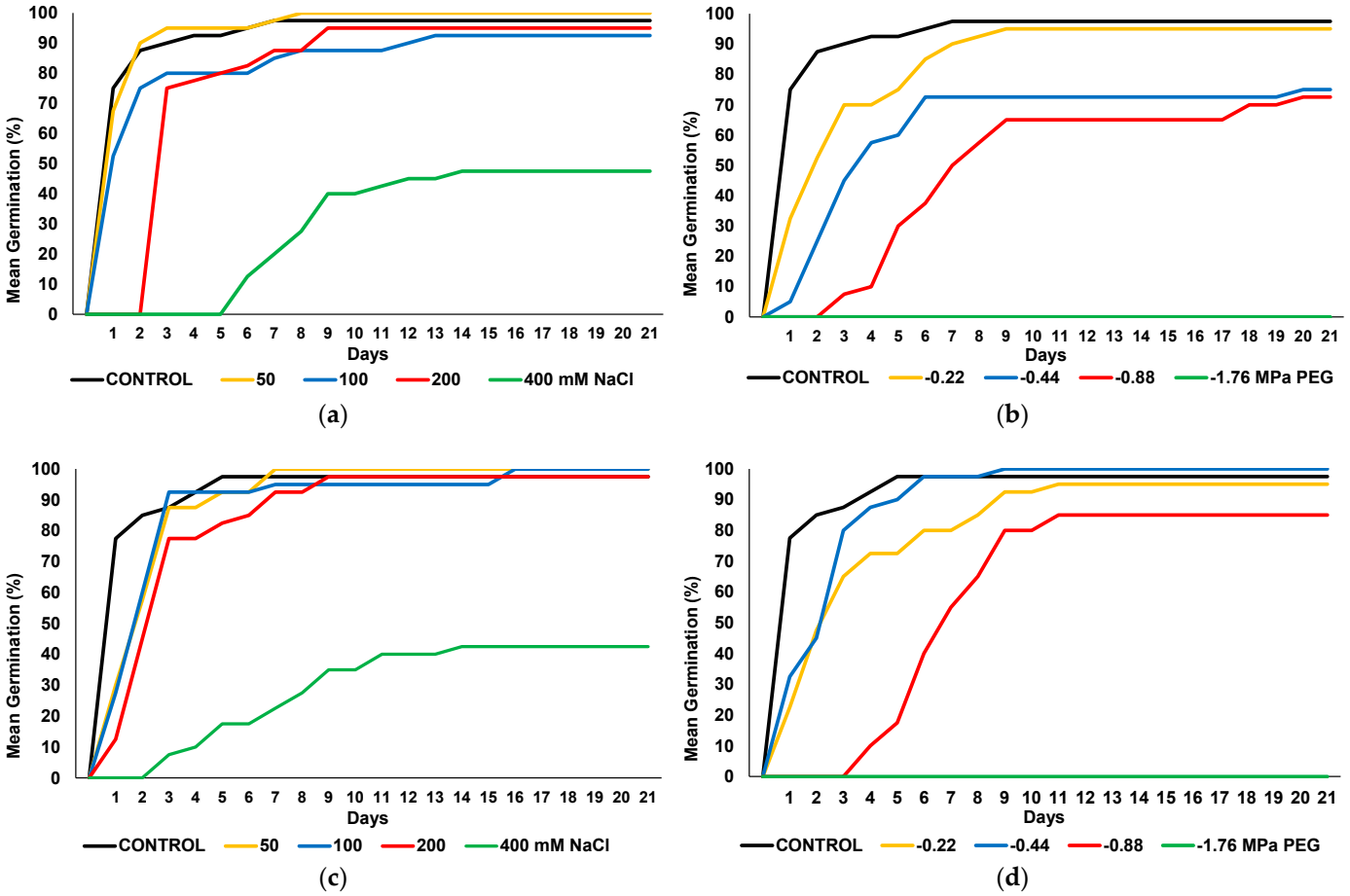

Figure 1. Evolution of germination during 21 days in *Ipomoea purpurea* under increasing concentrations of NaCl (**a**) and polyethylene glycol PEG 6000 (**b**) and in *Ipomoea tricolor* under increasing concentrations of NaCl (**c**) and polyethylene glycol PEG 6000 (**d**).

The two species showed a very high germination percentage under control conditions in distilled water: 97.50% for *I. purpurea* (Figures 1a and 2a) and 96.66% for *I. tricolor* (Figures 1c and 2b). Under salt stress conditions, high germination percentages above 90% were recorded in all salt treatments, except for 400 mM NaCl, for which only 47.5% of *I. purpurea* seeds (Figures 1a and 2a) and 42.5% of *I. tricolor* seeds (Figures 1c and 2b) were able to germinate after 21 days of treatment. Under isosmotic PEG concentrations at −1.76 MPa, seeds did not germinate at all when PEG was applied (Figure 1b,d and Figure 2). At −0.44 and −0.88 MPa, mean germination percentages of 75% and 72.5% were recorded in *I. purpurea* and *I. tricolor* seeds, respectively, lower but not significantly different from the non-stressed controls (Figure 1b,d and Figure 2).

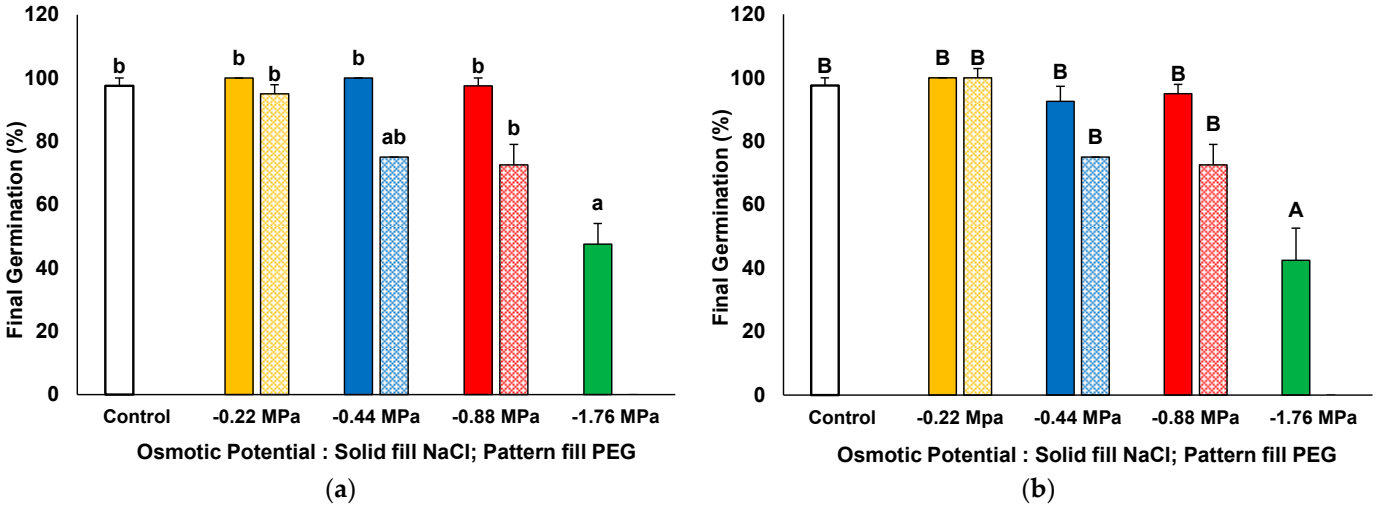

Figure 2. Final germination percentages in *Ipomoea purpurea* (**a**) and *I. tricolor* (**b**) after 21 days of treatment with increasing iso-osmotic concentrations of NaCl and PEG. Control: germination in distilled water. The values plotted are the means ± SE (n = 4). Different lowercase and uppercase letters within the bars indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

In addition to germination percentages, germination speed was calculated as mean germination time (MGT). Both species had very fast germination in the absence of stress, as low as 1.5 days (Figure 3). For both species, MGT increased gradually in parallel to the increase in NaCl concentration in the germination medium. However, significant differences were only observed for 400 mM NaCl, reaching 8.7 and 7.8 days in *I. purpurea* (Figure 3a) and *I. tricolor* (Figure 3b), respectively. On the other hand, the effect of PEG on germination time was stronger than that of NaCl since a significant increase of close to 7 days in both species was registered at a PEG osmotic potential of −0.88 MPa (Figure 3).

Other germination parameters, such as the first day of germination (FGD), last day of germination (LGD), and total spread of germination (TSG), indicate that the two species have very rapid germination in the absence of stress. For both species under control conditions, germination started on the first day and finished before the fifth day (Table 1) of the trial. Indeed, a shorter TSG was found in *I. purpurea* (2.8) than in *I. tricolor* (3.5) (Table 1). A significant germination delay was recorded for *I. purpurea* at −0.88 MPa, either with salt or PEG treatments (Table 1). In contrast, for *I. tricolor*, it was only observed at −1.76 MPa (Table 1). Although a delay in the last day of germination and an extension of the germination spread were recorded in both species under NaCl and PEG, these were not significantly different from the control due to the large variability between replicates.

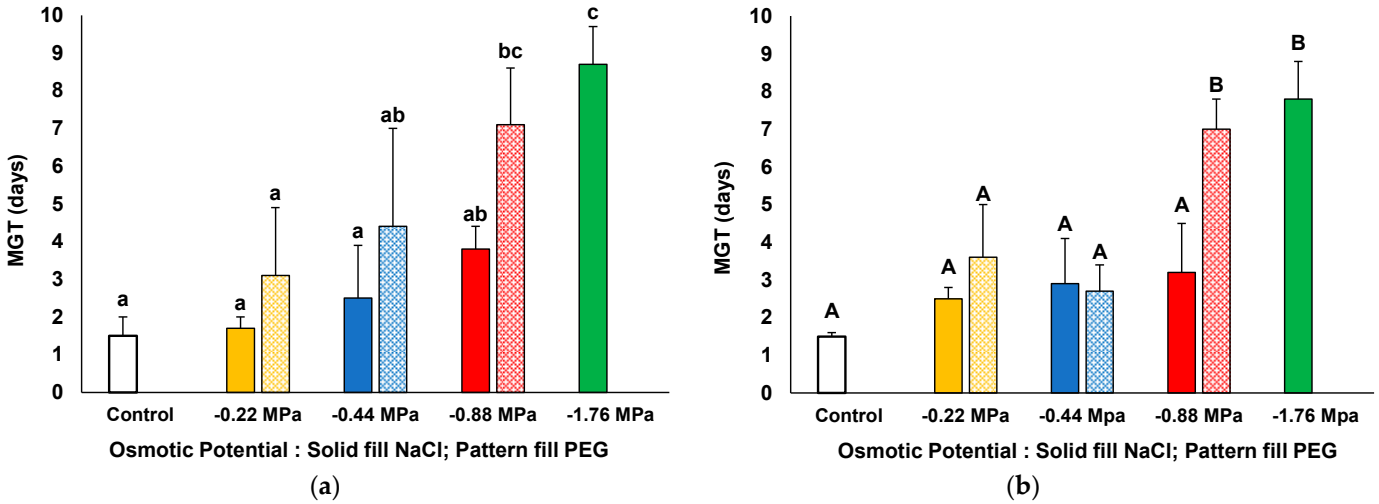

Figure 3. Mean germination time (MGT) in *I. purpurea* (**a**) and *I. tricolor* (**b**) after 21 days of treatment with increasing iso-osmotic concentrations of NaCl and PEG. Control: germination in distilled water. The values plotted are the means ± SE (n = 4). Different lowercase and uppercase letters within the bars indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$). For both species, no germination was observed for PEG treatments equivalent to −1.79 MPa; thus, no MGT is measured and plotted for this condition.

Table 1. Germination parameters related to the velocity of germination. Control: germination in distilled water. Values are the means ± SE (n = 4). Different lowercase and uppercase letters indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

Species	Osmotic Potential	Treatment	First Day of Germination (FGD)	Last Day of Germination (LGD)	Total Spread of Germination (TSG)
I. purpurea	0	Control	1.0 ± 0.0 a	3.8 ± 1.1 a	2.8 ± 1.1 a
	−0.22 MPa	NaCl	1.0 ± 0.0 a	5.0 ± 1.4 a	4.0 ± 1.4 a
	−0.44 MPa	NaCl	1.0 ± 0.0 a	7.5 ± 3.1 a	6.5 ± 3.1 a
	−0.88 MPa	NaCl	3.0 ± 0.0 bc	7.5 ± 1.5 a	4.5 ± 1.5 a
	−1.76 MPa	NaCl	7.3 ± 1.2 d	10.3 ± 1.2 a	3.0 ± 0.0 a
	−0.22 MPa	PEG	1.5 ± 0.5 ab	6.5 ± 1.3 a	5.0 ± 1.0 ab
	−0.44 MPa	PEG	2.3 ± 0.6 ab	9.5 ± 3.5 a	7.3 ± 2.9 a
	−0.88 Mpa	PEG	4.0 ± 0.5 c	13.5 ± 2.5 a	9.5 ± 2.6 a
	−1.76 Mpa	-	-	-	-
I. tricolor	0	Control	1.0 ± 0.0 A	4.5 ± 0.2 A	3.5 ± 0.2 A
	−0.22 Mpa	NaCl	1.0 ± 0.0 A	6.5 ± 0.5 A	5.5 ± 0.5 A
	−0.44 Mpa	NaCl	1.0 ± 0.0 A	7.3 ± 3.0 A	6.3 ± 3.0 A
	−0.88 MPa	NaCl	1.5 ± 0.2 A	6.0 ± 1.7 A	4.5 ± 1.4 A
	−1.76 MPa	NaCl	5.8 ± 1.1 B	11.0 ± 0.8 A	5.3 ± 1.6 A
	−0.22 MPa	PEG	1.0 ± 0.0 A	8.0 ± 1.2 A	7.0 ± 1.2 A
	−0.44 MPa	PEG	1.0 ± 0.0 A	5.5 ± 1.3 A	4.5 ± 1.3 A
	−0.88 Mpa	PEG	4.5 ± 0.5 B	9.5 ± 0.5 A	5.0 ± 0.0 A
	−1.76 MPa	PEG	-	-	-

After 21 days, the seedlings' length was analysed by measuring radicle and hypocotyl length separately (Table 2). Although radicle emergence was observed in seeds subjected to the highest NaCl concentration (400 mM) in the two species, the radicle did not grow over 2–3 mm, and seedlings were not viable. Thus, the osmotic potential of −1.76 MPa inhibited post-germination development under NaCl and PEG treatments in the two species. In *I. purpurea*, radicle length was significantly reduced, starting with the −0.88 MPa osmotic potential generated by PEG and NaCl, but hypocotyl length was significantly reduced in all stress treatments. The seedling vigour index (SVI) decreased significantly, starting with the −0.44 MPa osmotic potential treatment. Germination under 400 mM NaCl was blocked and was not even initiated in the PEG treatment at the same osmotic potential in *I. purpurea* and *I. tricolor*. However, in the latter species, radicle and hypocotyl length did not undergo significant reductions with respect to the control under all other experimental conditions tested; also, a significant reduction in SVI was only observed at an osmotic potential of −0.88 MPa (Table 2). Thus, *I. tricolor* showed better resistance to high osmotic pressure provoked by NaCl and PEG than *I. purpurea*.

Table 2. Seedlings analysis after 21 days, at the end of the germination assays. Control: germination in distilled water. Values are the means ± SE (n = 4). Different lowercase and uppercase letters indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

Species	Osmotic Potential	Treatment	Radicle Length (mm)	Hypocotyl Length (mm)	Seedling Vigour Index (SVI)
I. purpurea	0	Control	56.1 ± 1.8 c	39 ± 1.4 d	92.8 ± 1.6 c
	−0.22 MPa	NaCl	44.7 ± 3.1 bc	25.2 ± 2.8 c	70.0 ± 5.4 bc
	−0.44 MPa	NaCl	39.5 ± 2.9 bc	20.2 ± 2.4 c	55.1 ± 4.9 b
	−0.88 MPa	NaCl	15.0 ± 3.8 a	7.2 ± 0.8 a	21.4 ± 4.9 a
	−1.76 MPa	NaCl	-	-	-
	−0.22 MPa	PEG	60.8 ± 12.2 c	13.3 ± 1.7 b	71.2 ± 14.4 bc
	−0.44 MPa	PEG	40.9 ± 15.7 bc	8.6 ± 1.9 ab	43.1 ± 19.6 ab
	−0.88 MPa	PEG	28.3 ± 4.1 ab	7.2 ± 1.0 a	24.9 ± 0.7 a
	−1.76 MPa	PEG	-	-	-
I. tricolor	0	Control	61.3 ± 3.6 A	25.7 ± 0.6 A	85.0 ± 4.8 CD
	−0.22 MPa	NaCl	66.9 ± 3.5 A	20.5 ± 0.9 A	87.4 ± 4.3 CD
	−0.44 MPa	NaCl	53.2 ± 5.5 A	22.4 ± 2.0 A	75.6 ± 6.6 BC
	−0.88 MPa	NaCl	44.5 ± 10.2 A	13.4 ± 0.8 A	56.7 ± 9.9 AB
	−1.76 MPa	NaCl	-	-	-
	−0.22 MPa	PEG	65.3 ± 7.7 A	13.5 ± 1.7 A	75.6 ± 10.4 BC
	−0.44 MPa	PEG	68.9 ± 20.2 A	37.5 ± 23.6 A	106.4 ± 10.9 D
	−0.88 MPa	PEG	42 ± 6.3 A	14.5 ± 0.8 A	48.4 ± 7.3 A
	−1.76 MPa	PEG	-	-	-

3.2. Plant Growth

Both species had rapid growth, increasing during the three weeks of treatments by 105 cm in *I. purpurea* and 126 cm in *I. tricolor* (Figure 4b), reaching heights at the harvest date of 1.96 m for the former and 2.2 m for the latter. The roots were considerably shorter than the aerial part and showed a similar size in *I. purpurea* and *I. tricolor* under control conditions, circa 91 cm and 74 cm, respectively (Figure 4a). Plant growth was inhibited under stress conditions for both species, mainly by water stress followed by the higher salt concentration, but not so much by the 100 mM NaCl solution. For instance, the growth

of *I. purpurea* roots was reduced 3-fold by water stress and high (i.e., 200 mM NaCl) salt concentration, whereas water stress but not salt stress treatment shortened *I. tricolor* roots (Figure 4a). On the other hand, the increase in stem length, calculated as the differences between final and initial stem length, revealed only a significant 1.6-fold reduction in the water-stressed *I. tricolor* plants (Figure 4b).

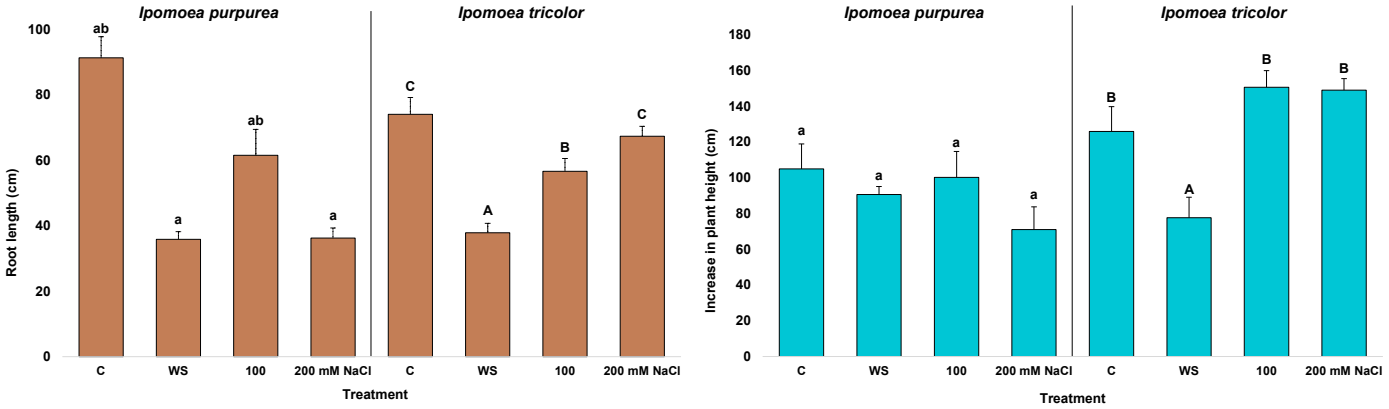

Figure 4. Root length (**a**) and increase in stem length (**b**) after three weeks of treatment in the two *Ipomoea* species. The values plotted are the means ± SE (n = 5). Different lowercase and uppercase letters indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

The fresh weight (FW) of roots, stems, and leaves was registered. The highest FW was found in the two species in the absence of stress, with an average total FW of 37 g in *I. purpurea* and 42 g in *I. tricolor*. Under stress, a similar pattern of variation was found in the two species, with the strongest effect induced by the water stress treatment, followed by 200 mM NaCl (Figure 5a). Specifically, under water stress, there was a marked 14-fold reduction in *I. purpurea* root FW, an 11-fold reduction in *I. tricolor* root FW, a 3.2- and 4.3-fold reductions in leaf FW, and a 1.4- and a 2.2-fold in steam FW registered for *I. purpurea* and *I. tricolor*, respectively (Figure 5a). Only a small variation with respect to control plants was recorded in 100 mM NaCl growing plants, significant only in *I. purpurea* roots (Figure 5a).

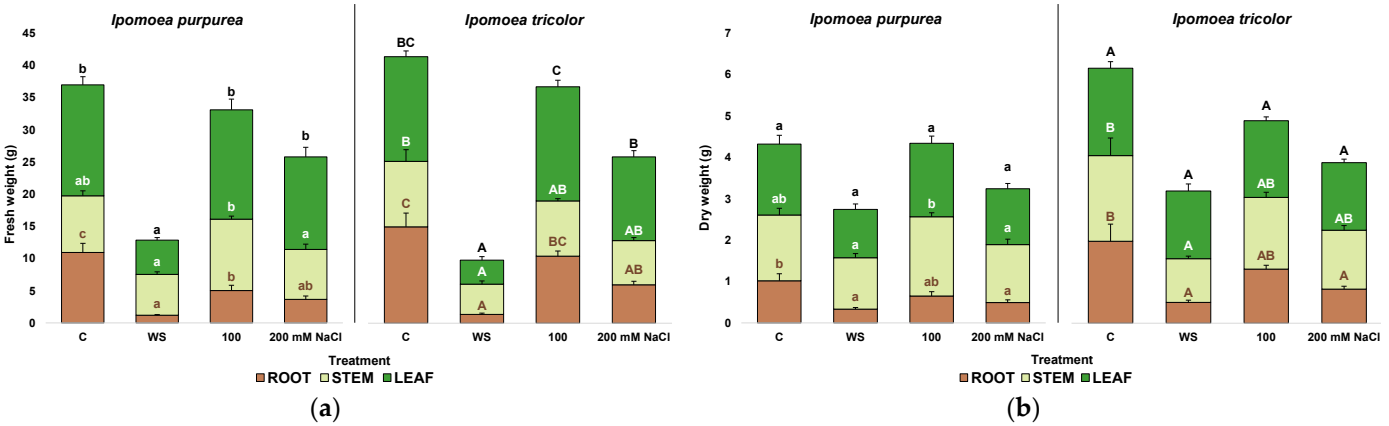

Figure 5. Fresh weight (**a**) and dry weight (**b**) of roots, stems and leaves after three weeks of treatment in the two *Ipomoea* species. The values plotted are the means ± SE (n = 5). Different lowercase and uppercase letters indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

Similarly, the dry weight of roots, stems, and leaves was registered. The highest dry weight values for roots, stems, and leaves were found in plants grown under control conditions, slightly lower for *I. purpurea* than in *I. tricolor* plants (Figure 5b). These values agree with the fresh weight values observed (Figure 5a). The pattern of DW variation in plants subjected to stress treatments was similar to that of FW, although reductions between treatments were not as marked. The most significant DW decrease was recorded in water-stressed plants, especially in roots (3-fold in *I. purpurea* and 4-fold in *I. tricolor*, Figure 5b). Salt treatments had no effect in stem and leaf DW, neither in *I. purpurea* nor *I. tricolor*, and significant losses were only registered in the roots of plants treated with 200 mM NaCl for both species (Figure 5b).

The smaller reduction in dry weight than in fresh weight was related to the water loss under the stress treatment, shown in Figure 6. The strongest dehydration occurred in the plants of the water stress treatments, where significant variations from the control were recorded in the water content of roots and leaves but not of stems. *I. purpurea* plants under water stress showed a 1.6 and 1.1-fold reduction compared to the control in roots and leaves, respectively (Figure 6a), whereas in *I. tricolor* the water loss was more pronounced in leaves (1.6-fold) than in roots (1.4-fold; Figure 6b).

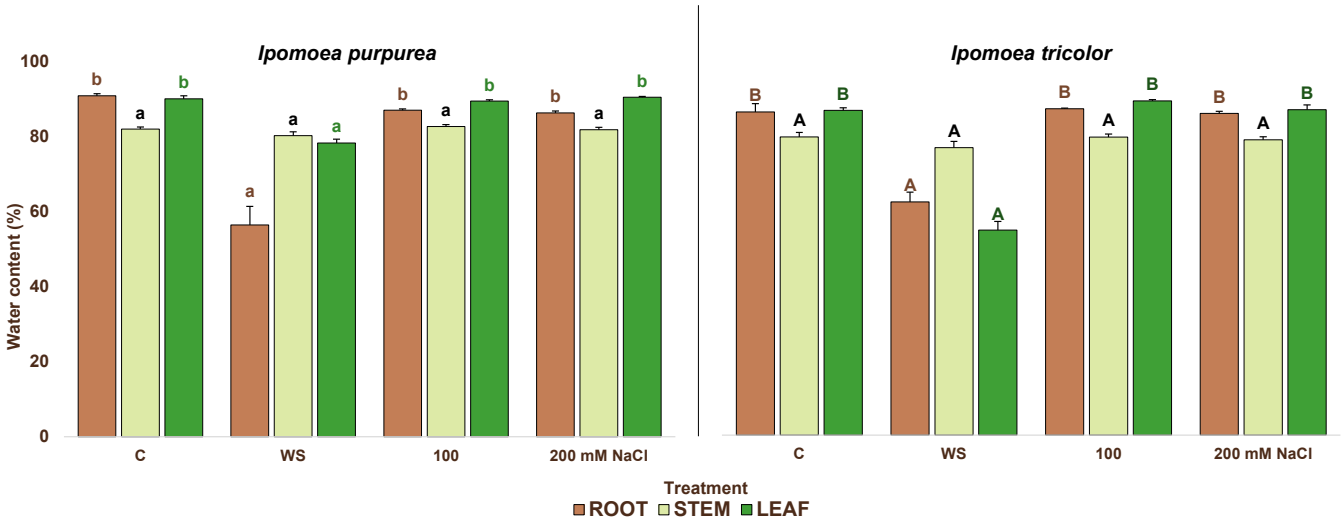

Figure 6. Water content in roots, stems, and leaves in *I. purpurea* (**a**) and *I. tricolor* (**b**) after three weeks of treatment in the two *Ipomoea* species. The values plotted are the means ± SE (n = 5). Different lowercase and uppercase letters indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

3.3. Photosynthetic Pigments

The highest concentration of leaf photosynthetic pigments was recorded in plants grown under control conditions. Chlorophyll values were higher in *I. purpurea* than in *I. tricolor* (8.74 and 5.35 mg/g DW), whereas chlorophyll *b* concentrations were similar (Figure 7a). Carotenoid concentrations were also higher in *I. purpurea* (1.5 mg/g DW) than in *I. tricolor* (1.0 mg/g DW) (Figure 7b). Salinity but no water stress had a negative effect on chlorophyll *a* and carotenoid concentrations in *I. purpurea*, whereas *I. tricolor* accumulated similar pigment concentrations under all growing conditions (Figure 5a,b). Chlorophyll *b* concentrations were constant for both species in all treatments.

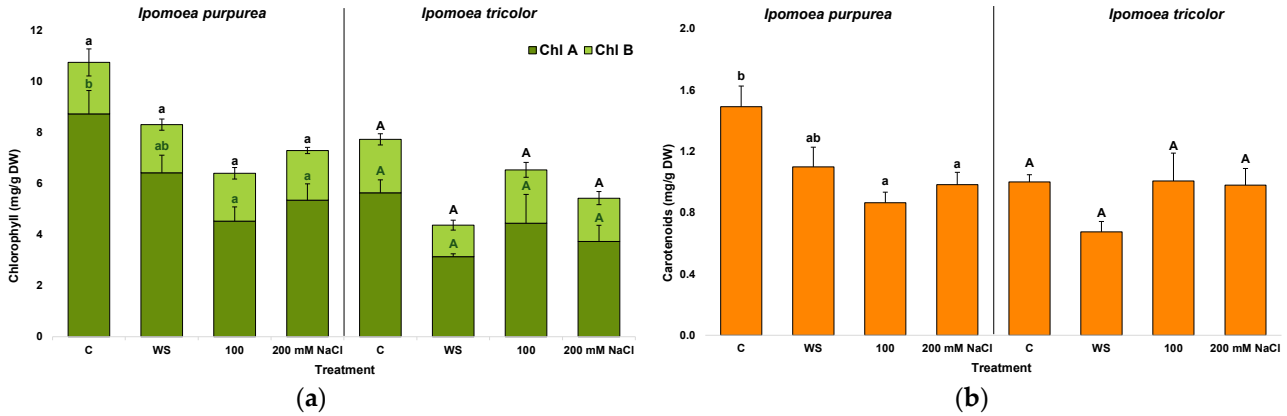

Figure 7. Chlorophylls *a* and *b* (**a**) and carotenoids (**b**) after three weeks of treatment in the two *Ipomoea* species. The values plotted are the means ± SE (n = 5). Different lowercase and uppercase letters indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

3.4. Ion Contents

As expected, an increase in Na^+ and Cl^- concentrations were only found in the salt-treated plants but not in the water stress treatment (Table 3). However, the pattern of Na^+ accumulation was different in the two species. In *I. purpurea* roots, a significant 2.3- and 1.8-fold increase was measured in 100 and 200 mM NaCl-treated plants, respectively, but no variation was observed in leaves, neither in water-stressed nor salt-treated plants (Table 3). Surprisingly, an opposite pattern was observed for *I. tricolor*; Na^+ concentrations increased significantly only in the leaves of salt-treated plants (1.7-fold higher in 200 mM NaCl-treated plants, compared to control plants) but not in the roots (Table 3). On the other hand, Cl^- concentration measured in the two species increased significantly in roots and leaves in the salt stress treatments but not in the water-stressed plants. Only *I. tricolor* grown under water stress showed a significant decrease of Cl^- in roots (Table 3). A difference in the accumulation pattern of these two monovalent ions was observed in the two species, Na^+ concentrations were substantially higher in roots than in leaves, whereas Cl^- concentrations were similar in both organs.

Table 3. Root and leaf ion concentrations after three weeks of treatment in plants of the two *Ipomoea* species. The values are the means ± SE (n = 5). Different lowercase and uppercase letters indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

Ion	Treatment	*I. purpurea*	*I. tricolor*
Na^+ roots (µmol/g)	C	963.6 ± 102.3 a	1028.3 ± 55.3 A
	WS	821.3 ± 34.0 a	946.7 ± 73.9 A
	100 mM NaCl	2185.4 ± 163.4 b	1440.9 ± 189.6 A
	200 mM NaCl	1714.0 ± 261.4 b	1298.4 ± 153.7 A
Na^+ leaves (µmol/g)	C	522.9 ± 84.8 a	426.6 ± 108.5 A
	WS	473.8 ± 39.4 a	347.5 ± 54.0 A
	100 mM NaCl	409.0 ± 34.7 a	583.4 ± 34.6 AB
	200 mM NaCl	531.6 ± 26.4 a	732.2 ± 48.6 B
K^+ roots (µmol/g)	C	503.1 ± 71.2 b	553.5 ± 59.8 B
	WS	573.1 ± 24.7 b	563.5 ± 23.8 B
	100 mM NaCl	278.5 ± 32.2 a	219.0 ± 57.7 A
	200 mM NaCl	250.5 ± 23.4 a	132.5 ± 16.3 A

Table 3. *Cont.*

Ion	Treatment	*I. purpurea*	*I. tricolor*
K^+ leaves (µmol/g)	C	518.4 ± 41.4 a	649.8 ± 93.5 AB
	WS	507.2 ± 18.2 a	576.2 ± 81.6 A
	100 mM NaCl	555.4 ± 45.3 a	920.4 ± 51.3 BC
	200 mM NaCl	656.2 ± 67.3 a	995.4 ± 38.9 C
Cl^- roots (µmol/g)	C	442.1 ± 63.1 a	520.8 ± 65.4 A
	WS	429.5 ± 44.5 a	456.3 ± 30.3 B
	100 mM NaCl	1986.0 ± 175.4 b	1655.4 ± 171.9 B
	200 mM NaCl	1977.9 ± 169.5 b	1352.7 ± 150.7 B
Cl^- leaves (µmol/g)	C	663.3 ± 40.6 a	439.6 ± 72.0 A
	WS	649.3 ± 51.3 a	313.1 ± 48.9 A
	100 mM NaCl	1610.8 ± 103.4 b	2029.4 ± 178.1 B
	200 mM NaCl	1624.9 ± 75.9 b	1978.5 ± 141.0 B
Ca^{2+} roots (µmol/g)	C	74.5 ± 8.7 a	79.0 ± 6.4 A
	WS	59.6 ± 2.8 a	49.1 ± 0.9 A
	100 mM NaCl	305.1 ± 43.6 b	257.7 ± 33.7 B
	200 mM NaCl	283.9 ± 35 b	226.6 ± 49.1 B
Ca^{2+} leaves (µmol/g)	C	259.4 ± 59.9 ab	126.8 ± 35.0 A
	WS	151.3 ± 34.4 a	77.7 ± 14.0 A
	100 mM NaCl	267.4 ± 67.5 ab	411.4 ± 32.0 B
	200 mM NaCl	399.3 ± 28.4 b	362.3 ± 38.7 B

A significant decrease in K^+ concentrations was measured in the roots of salt-treated plants of both species but not in those of water-stressed plants (Table 3). K^+ concentration in the roots of 200 mM NaCl-treated *I. purpurea* plants was reduced by ca. 50% with respect to control plants, and an even more substantial decrease was observed in *I. tricolor*. Regarding leaf K^+ levels, they were not affected by the water or salt stress treatments in *I. purpurea* but increased significantly in plants of *I. tricolor* grown in the presence of 200 mM NaCl (Table 3). In non-stressed control plants, K^+ concentrations were similar in roots and leaves.

Finally, Ca^{2+} levels in control plants were higher in leaves than in roots, about 3.5- and 1.6-fold in *I. purpurea* and *I. tricolor*, respectively. In both species, Ca^{2+} root or leaf contents were not significantly affected by the water stress treatment but increased in response to salt stress (Table 3).

3.5. Osmolytes Contents

Proline (Pro) and total soluble sugars (TSS) were quantified in the leaf tissue of all plants harvested after the different treatments. In *I. purpurea*, no significant differences were found in Pro contents between control and water-stressed or salt-stressed plants (Figure 8a, left). On the contrary, in *I. tricolor* Pro increased significantly, ca. 18-fold over control values, in plants subjected to water stress; salt stress also induced the accumulation of Pro, although to a lesser extent and with significant differences with respect to non-stressed controls observed only in the 200 mM NaCl-treated plants (Figure 8a, right). In any case, it should be pointed out that absolute Pro values are too low to have any significant osmotic effect.

A different pattern was observed for TSS contents, which decreased significantly in *I. purpurea* plants subjected to water stress and increased in response to salt treatments, especially at 100 mM NaCl (Figure 8b, left). On the other hand, in *I. tricolor*, TSS levels did not vary significantly in the stressed plants with respect to those grown under control conditions (Figure 8b, right).

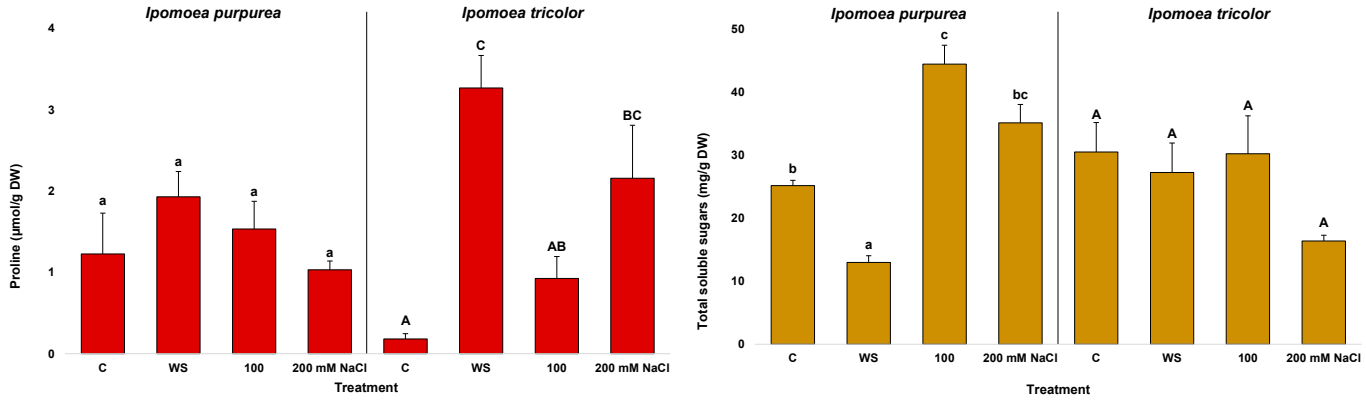

Figure 8. Proline (**a**) and total soluble sugars (**b**) after three weeks of treatment in the two *Ipomoea* species. The values plotted are the means ± SE (n = 5). Different lowercase and uppercase letters indicate significant differences between treatments, for each species, according to the Tukey post hoc test ($p < 0.05$).

3.6. Multivariate Analysis

The mean values of the germination and seedling data were used in a Principal Component Analysis (PCA). The variables considered were clustered by the PCA and reduced to two main components with an eigenvalue greater than one, which together accounted for 86.65% of the total variability. The loading plots of the vectors and the scores of the two species in relation to these components are shown in Figure 9. Most of the overall variability of the analysed data was explained by the first component (72.74%). The variables with a positive correlation with the highest weight value in this component were the germination percentage, hypocotyl length (HL), and seedling vigour index (SVI). The variables related to the speed of germination, namely the first germination day (FGD), the last germination day (LGD), and the mean time of germination (MG), were negatively correlated. The first component separated the scores from the control treatments on its positive side and those of lower osmotic potential on the negative side. The second component, explaining an additional 13.90% of the total variability, was positively correlated with radicle length (RL) and the total spread of germination (TSG) and negatively correlated with the final percentage of germination (Germ %). The scores of *I. purpurea* at −0.88 MPa osmotic potential were separated along the OY axis, with the PEG score on the positive and the NaCl score on the negative extreme.

Growth and biochemical parameters were combined in a second PCA (Figure 10). Only variables that changed significantly were taken into consideration. Four components had an eigenvalue higher than one, accounting for 95% of the total variability. The first, explaining 42.74% of the variation, was positively correlated with the fresh weight of leaves (FWl), the water content of leaves (WCl) and Ca^{2+} concentrations in roots and leaves, and negatively correlated with K^+ in roots. The second axis, explaining 25.97% of the data variability, was positively related to root length (RL), root fresh weight (FWr), root dry weight (DWr) and chlorophyll *a* and negatively correlated with proline (Pro), Ca^{2+} and Cl^- in roots.

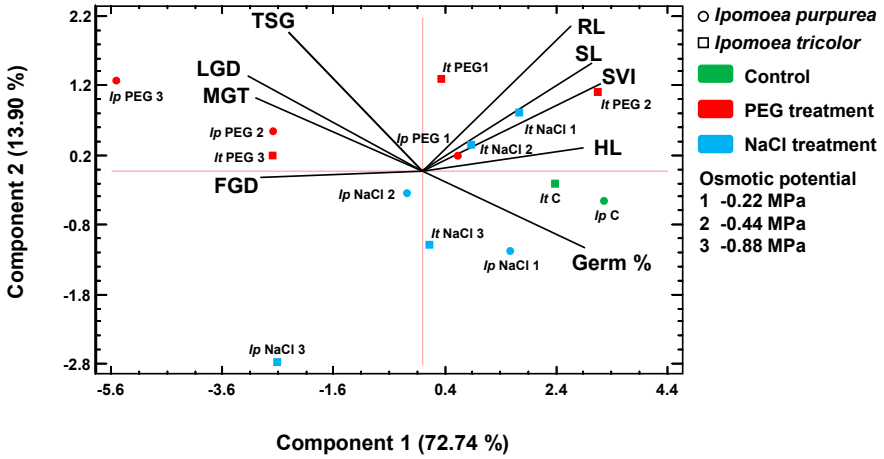

Figure 9. Principal Component Analysis of germination data of *I. purpurea* and *I. tricolor*. Loading and scatter plots of the PCA scores were conducted with germination and seedling traits. Abbreviations: Germ %, final percentage of germination; MGT, mean germination time; FGD, first germination day; LGD, last germination day; TSG, total spread of germination; RL, radicle length, RL; HL, hypocotyl length; SL, seedling length; SVI, seedling vigour index.

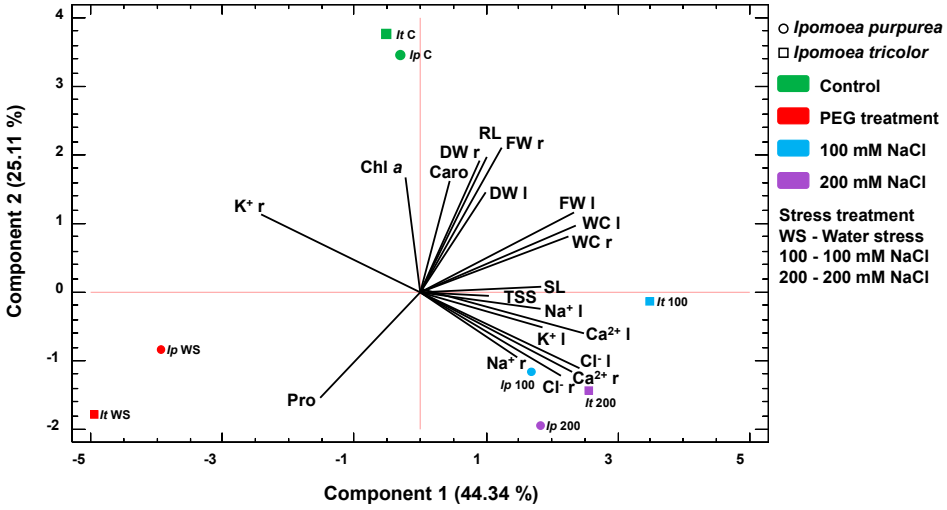

Figure 10. Principal Component Analysis of growth and biochemical data of *Ipomoea purpurea* and *I. tricolor*. Loading and scatter plots of the PCA scores were conducted only with the parameters that showed a significant correlation. Abbreviations: C, control; 100, 100 mM NaCl; 200, 200 mM NaCl; WS, water stress; FW r, root fresh weight; FW l, leaf fresh weight; DW r, root dry weight; DW l, leaf dry weight; WC r, root water content; WC l, leaf water content; Chl a chlorophyll *a*; Caro, carotenoids; Pro, proline; TSS, total soluble sugars; Na r, root sodium content; Na l, leaf sodium content; K r, root potassium content; K l, leaf potassium content; Cl r, root chlorine content; Cl l, leaf chlorine content; Ca r, root calcium content; Ca l, leaf calcium content.

4. Discussion

High seed production and efficient vegetative propagation are common traits of invasive species, regardless of their phylogenetic relationships or ecology. Sexually reproducing invasive species usually produce a large number of seeds, ensuring a high rate of offspring. However, their ability to germinate earlier and faster is more relevant than their usually high germination rates [47–49]. The two *Ipomoea* species tested showed a very high germination percentage in the absence of stress, which is a common trait in commercial seeds of ornamental species. However, the most remarkable feature was their very

rapid germination, with a high percentage of seeds already germinated on the first day, whereby a very short germination spread (TSG) was found, especially in *I. purpurea*, with an average of 2.8 days. Rapid germination is a functional trait that confers advantages in the early stages of interspecific competition [50,51]. Invasive species of ornamental origin are favoured by a selective introduction [51,52], with horticulture being the largest source of plant invasions [20]. The two *Ipomoea* species were also characterised by rapid seedling growth, which may play an additional role in outcompeting species with slower germination and seedling development [51]. Another exceptionally relevant trait characterising many invasive species is their ability to germinate in a wide range of environmental conditions [51,53–55]. Global warming is increasing the risk of exposure to unfavourable conditions and favours species with greater abiotic resistance. Comparison of germination success under environmentally constrained conditions between native and invasive species revealed in many cases that the latter have wider ranges of tolerance to temperatures and water potentials [56,57]. Low water availability delayed the germination of alien species less than that of native species coexisting in the same habitat in SW Australia [58], and salinity did not affect germination rates of woody invasive species in inland soils of the Mississippi region, contributing to the spread of these species [59]. The invasive *Spartina densiflora* in SW Spain had a broader range of salt tolerance than a cordgrass species native to the SW Iberian Peninsula [60], and its seeds germinated even at the hypersaline conditions of 0.75 M NaCl. The two *Ipomoea* species analysed here maintained over 90% germination in saline solutions up to 200 mM NaCl. In the treatment with 400 mM NaCl over 40% of seed-initiated germination was measured as radicle emergence, but their development was stopped immediately as this concentration was lethal for all seedlings. Seeds also germinated in the treatment with increasing concentrations of PEG, but in the two species, the percentage of germination at low osmotic potentials was reduced than in the salt treatments. Salinity affects germination due to the accumulation of toxic levels of Na^+ and Cl^- and to its osmotic component, as increased osmotic potential prevents water uptake and alters water imbibition by seeds [61,62]. Germination in polyethylene glycol (PEG) solutions is the standard method to test this osmotic effect, which mimics environmental drought conditions [54,63]. Similar findings indicating that germination is more affected by osmotic stress than by ionic toxicity have been previously reported in *I. purpurea* [64–66]. Additionally, in agreement with the results shown here, high germination percentages under salt stress conditions were found in this species [65,66], as in others of this genus [67,68]. A comparative study on several environmental constraints in *I. purpurea* revealed that germination was more affected by temperature than by salinity and seedling emergence by flooding and burial depths of over 13 cm [69]. The two species analysed here had similar germination patterns and percentages, except germination at −0.88 MPa osmotic potential in *I. purpurea*, which was more affected by stress than *I. tricolor*. The seedlings analysis also indicated a relatively higher tolerance to NaCl and PEG of the latter, as only in *I. purpurea* stress treatments significantly reduced the length of radicle and hypocotyl.

The two species have not only a high velocity of germination but also fast growth. *I. purpurea* has been reported to have a growth of about 20 cm per day under optimal conditions [70], although, under our growing conditions, an average increase of only 5 cm daily was recorded in plants from the control treatments. A higher growth rate of about 6 cm/day in control and 7 cm/day in plants from the 100 mM NaCl was found in *I. tricolor*. Quick growth is an essential trait of weeds [71] often associated with the species' invasive potential [72]. In circumstances where there is competition, plants that grow faster have an advantage as they can emerge from the vegetation to exploit photosynthetic resources [73]. Both *Ipomoea* species are vining weeds, able to compete by "choking growth" [70]. Growth of the two species was not hampered at 100 mM NaCl and only a few parameters were significantly reduced at 200 mM, indicating that the two species are moderately salt-tolerant. Salt tolerance is a common trait in this genus, which has been reported in species such as the littoral or wetland species *I. cairica* [74], *I. sagittata* [75], *I. pescaprae* [76], or even in the

sweet potato *I. batatas* [77]. However, the growth of the two species was severely affected by lack of irrigation, as reflected in the significant reduction of most of the traits analysed, as previously reported in *I. purpurea* [78]. Severe drought, in combination with leaf damage, had a drastic effect on the growth of this species [79], but other studies indicate a substantial plasticity of its ecophysiological traits [80].

Biochemical analysis indicated a variation of photosynthetic pigments in stressed plants, but significant reductions in chlorophyll *a* and carotenoids were only observed in *I. purpurea*, indicating a possible higher tolerance of *I. tricolor*, where only small, non-significant fluctuations were observed between treatments. Total chlorophyll and carotenoid concentrations correlated well with growth parameters and were recommended as reliable stress markers in multi-parameter assessments in the congener *I. aquatica* [81].

The compatible solutes analysed, proline (Pro) and total soluble sugars (TSS), showed a different pattern in the two species. Proline contents increased significantly, especially in *I. tricolor* plants subjected to water stress, followed by those subjected to 200 mM NaCl. A smaller and not significant increase was registered in *I. purpurea*, but its levels of Pro in control plants were considerably higher than in the other species, which had only a low content in the absence of stress. On the other hand, TSS increased significantly only in *I. purpurea* plants subjected to salt treatments. Proline, one of the most common osmolytes in plants, has an essential role in stress responses [82]. In addition to its function in osmotic adjustment, Pro plays multiple additional functions under stress, such as acting as a low-molecular-weight chaperone, metal chelator, ROS scavenger involved in antioxidant defence mechanisms, or signalling molecule [82–84]. The maximum absolute Pro concentrations reached in the two *Ipomoea* species are insufficient to produce a significant osmotic effect but are in the same range as those reported in the halophyte *I. pescaprae* [85]. However, there is evidence of Pro implication in stress tolerance in species of this genus, based on its additional biological functions. In a study on transgenic sweet potatoes, plants overexpressing IbSIMT1 accumulated more proline, which improved their salt tolerance not only by maintaining osmotic balance but also by activating SOD gene expression and enhancing ROS scavenging capacity [77]. Proline was reported to play an important role in drought resistance in *Ipomoea*, well documented in sweet potato and its hybrids [86–88]. Several publications also revealed the role of TSS in salt tolerance in sweet potatoes [87,89], although these compounds are involved in many physiological processes ranging from seed germination and flowering to plant senescence; therefore, variations in their concentrations are not always related to stress defence mechanisms [90,91].

Regulation of ion uptake and transport is of great importance in the response of plants to salinity stress. Halophytic dicots are generally salt includers, increasing the uptake and transport to the shoots of Na^+ and Cl^- where they are sequestered in vacuoles [92], whereas glycophytes and halophytic monocots are salt excluders. Their main mechanism of resistance to salt stress is to avoid the foliar accumulation of toxic ions, either by reducing the uptake by the roots or by blocking their transport to the aerial parts of the plant [93,94]. We detected differences between the two species in relation to the pattern of Na^+ accumulation. Under salt stress, the root levels of this cation increased in *I. purpurea*, but not in *I. tricolor* plants; in leaves, on the contrary, they were maintained in *I. purpurea* and increased in *I. tricolor* plants, although only under 200 mM NaCl, the highest salinity tested. Most important, leaf Na^+ concentrations were maintained lower in leaves than in roots under all tested experimental conditions. These data suggest the presence of mechanisms blocking Na^+ transport to the aerial part of the plants, slightly more efficient in *I. purpurea* than in *I. tricolor*, which could contribute to salt tolerance in these species. In contrast, Cl^- increased in both roots and leaves of the two species in response to salt and showed similar concentrations in roots and leaves.

Na^+ accumulation is generally accompanied by decreased intracellular K^+ levels, as the two cations compete for the same transporters, and increased Na^+ concentrations inhibit K^+-requiring enzymes [93]. K^+ plays an essential role in multiple physiological processes in plants, and its homeostasis is a general adaptive trait to different environmental stresses [95].

The primary survival mechanism of many glycophytes under saline conditions is the regulation of Na^+ transport and increased K^+ uptake and accumulation [96]. Following the general pattern of response to salt stress, a significant decrease in root K^+ content was observed in both *Ipomoea* species, somewhat more pronounced in *I. tricolor*. However, foliar K^+ concentrations remained constant in *I. purpurea* and even increased in 200 mM NaCl-treated plants of *I. tricolor*. This finding indicates that K^+ transport from the roots to the aerial part of the plants is activated under salt stress slightly more efficiently in *I. tricolor* than in *I. purpurea*, which probably represents a relevant tolerance mechanism in the two analysed species. Reports on other species of the genus support this idea. For example, a transcriptome profiling of salt-tolerant *I. imperati* revealed that one of the most promising genes for tolerance, *HKT1* (high-affinity potassium transporter), was over-represented in salt-stressed tissue libraries [97]. Moreover, in a comparative analysis of salt tolerance of 12 sweet potato genotypes, the more tolerant ones retained higher K^+ levels in their shoots under increasing salinity, revealing the importance of K^+ as the "main driver of salinity tolerance" in this species [98]. Salt and drought tolerance in transgenic sweet potato was enhanced by *IbNHX2*, a vacuolar Na^+/K^+ antiporter gen [99], whereas *NXH1* involved in the active transport of Na^+ and/or K^+ from the cytosol to the vacuoles was found to be responsible for an increased vacuolar pH in the petals of *I. tricolor*, which triggers a change in colour from purple-red to blue during flower opening [100].

Finally, the bivalent cation Ca^{2+} showed substantially higher concentrations in leaves than in roots in both species. Regarding changes in Ca^{2+} contents in response to the salt stress treatments, they increased significantly in the roots of the two species and the leaves only of *I. tricolor* plants. The role of Ca^{2+} in salt tolerance mechanisms is well established and has been previously reported, for example, in the related species *I. batatas* [89]. Calcium is crucial for the structure and functional integrity of plants, as it is involved in the stabilisation of membrane and cell wall structures, regulating ion transport and selectivity, or cell wall enzyme activities. Under stress conditions, Ca^{2+} is a key component of stress signalling pathways that trigger essential stress tolerance mechanisms, including accumulation of osmoprotectants, stimulation of antioxidants, polyamines and nitric oxide machinery [101].

5. Conclusions

The knowledge of the limits of stress tolerance of invasive species is extremely relevant, as they can predict how specific invasive species may behave under an altered climate and which new species may emerge as invasive. Our results indicate that the two *Ipomoea* species are relatively tolerant to salinity but susceptible to water stress in the analysed developmental stages, seed germination and vegetative growth. Salt tolerance is based mainly on blocking Na^+ while activating K^+ transport from roots to shoots and the uptake and accumulation of Ca^{2+} in response to increased soil salinity. The two species responded similarly to salt stress, although these tolerance mechanisms appear to be more efficient in *I. tricolor* than in *I. purpurea*, so the former species is slightly more tolerant. Currently, *I. purpurea* is generally recognised as a common invasive weed, whereas *I. tricolor* is considered 'low-risk', only locally reported as invasive. However, our results indicate that *I. tricolor* may have an invasive potential as high, if not higher than *I. purpurea*, and spread into new areas, affecting cropland or natural habitats of ecological interest with moderate salinity. Such studies could be applied to practice when monitoring natural areas of high ecological value, such as wetlands, where early warning and eradication programmes against stress-tolerant invasive species are necessary under changing climatic conditions.

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