

The effect of exposure to sea water on germination and vegetative growth of an epiphytic bromeliad

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Abstract: Vascular epiphytes can be quite abundant in vegetation close to the ocean surf, where they are exposed to a more or less continuous input of salt spray. The ecophysiological basis of their occurrence, i.e. salt tolerance or avoidance, is unresolved, because all previous studies were observational and conclusions thus circumstantial. Here, the effect of varying concentrations of salt water on germination, and growth and survival of seedlings and established plants was investigated in a growth cabinet study under controlled conditions. Seeds (1 500), seedlings (750) and small tank plants (336) were from four populations of *Werauhia sanguinolenta* that were growing either close to the sea or inland in Panama. Changes of Na⁺ and K⁺ concentrations in plant tissue were also determined. No differences in the sensitivity to salt were found among populations, nor among life stages. External concentrations (C_{ext}) of up to 15% sea water (c. 0.5% Na⁺) allowed complete germination as well as positive growth and survival in both seedlings and established plants over short periods (8–10 wk). After longer exposure (12 wk) of established plants visible damage and increased mortality were observed at lower C_{ext} , but critical tissue Na⁺ levels were similar: c. 50 mg gDW⁻¹. It is concluded that this common epiphyte does not meet the definition of a halophyte, but still possesses a rather high tolerance to sodium.

Key Words: Bromeliaceae, epiphytes, glycophyte, halophyte, heteroblasty, mangrove, nutrient limitation, Panama, RGR, seeds, *Werauhia sanguinolenta*

INTRODUCTION

Vascular epiphytes can be found in a variety of habitats, from dry forest in the lowlands to elfin forest, from forest in the centre of the Amazon basin to mangrove forest close to the sea (Benzing 1990, Graham & Andrade 2004, Zotz 2005). In the latter case, epiphytes are continuously exposed to ocean spray, and Gómez & Winkler (1991) suggested that the high abundance of epiphytes in some forests immediately adjacent to the sea is not due to any particular adaptation of these plants, but only possible because of high local precipitation which dilutes this constant input of salt. This is in line with a suggestion by Griffiths *et al.* (1989) that epiphytic bromeliads, which take up water and nutrients primarily or exclusively via absorbing leaf scales (Benzing 2000), lack the capacity to exclude uptake of potentially harmful ions and may thus be actually particularly sensitive to salt. On the

other hand, there is evidence that some epiphytes may be tolerant to substantial concentrations of harmful ions, particularly NaCl, in their tissues. For example, *Tillandsia usneoides* growing close to the sea in the southern USA had Na⁺ concentrations of up to 20% of ash without visible signs of damage (Shacklette & Connor 1973). Similarly, the Na⁺ concentrations exceeded that of K⁺ in *T. flexuosa* in a coastal plain in Venezuela (Griffiths *et al.* 1989), consistent with an observation made with *T. paucifolia* in Florida by Benzing & Renfrow (1971). Notably, the Na⁺ content of the latter species amounted to > 3% of dry matter. However, in a follow-up study with the same species (Benzing 1978), a much lower survival of seedlings in mangrove compared with hardwood forest was found, which could be due to a negative effect of high salt input.

Thus, our current understanding of the physiological basis of the occurrence of vascular epiphytes in habitats with substantial atmospheric salt input is still quite sketchy. Virtually all evidence is observational and all conclusions thus circumstantial. This motivated

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the present study in which a variety of physiological parameters were investigated in response to experimental manipulation. It is known from terrestrial species (Köhl 1997) that populations from saline habitats close to the coast may differ from inland populations. Assuming similar variation in the sensitivity to salt exposure among epiphytic taxa, we compared four different populations of a common Panamanian bromeliad varying in their natural exposure to salt spray. Finally, published evidence for epiphytes deals primarily with the response of large plants to salt. However, even among true halophytes salt tolerance varies with different stages of plant development (Ungar 1991), e.g. salt tolerance is about two orders of magnitude larger in adult *Atriplex halimus* than in seedlings (Mayer & Poljakoff-Mayber 1963). Seedlings may be quite susceptible to salinity in many species simply due to their small size, since tolerance may be either energetically expensive or be volume dependent (Leck *et al.* 2008). To account for such possible variation in salt tolerance during ontogeny we included germinating seeds, seedlings and established plants in our study.

METHODS

Plant material and experimental conditions

The bromeliad *Werauhia sanguinolenta* (Linden ex Cogn. & Marchal) Grant (syn. *Vriesea sanguinolenta* Cogn. & Marchal) is found from Costa Rica to Colombia and on various Caribbean islands in lowland to lower montane wet forests (Croat 1978, Schmidt & Zotz 2002, Zotz *et al.* 2005). The small seedlings of this heteroblastic species resemble atmospheric (i.e. possess non-impounding rosettes of small, linear leaves, which are densely covered by the shields of foliar trichomes), whereas larger conspecifics form tanks (i.e. feature broad leaves, which overlap basally forming water-filled chambers). We obtained material from four different populations in Panama. The first is growing on a small reef island (Cayo Zapatilla) off the coast of Panama in the Bocas del Toro province ('Bocas del Toro') with all collected plants growing < 10 m from the surf, the second population is from seasonal lowland forest of Barro Colorado Island ('BCI'), the third from lower montane rain forest in the Fortuna region ('Fortuna', c. 500 m asl), and the fourth from secondary vegetation in the lowlands in the Province of Veraguas ('Veraguas'). At each site, we collected small tanks (c. 5 cm longest leaf) and seed capsules from at least four different individuals. Plants were transferred to the University of Oldenburg, where they were kept in a growing house for 4 wk before the beginning of the experiment. Plants were watered regularly with deionized water. A subset (4 individuals per population) was dried

shortly after collection at 80°C for 72 h in a drying oven to establish a relationship between plant dry weight (DW) and fresh weight (FW, $15\% \pm 2\%$, $n = 16$). After digestion of the samples following standard procedures (Allen 2008) their Na^+ and K^+ concentrations were determined with an atomic absorption spectrophotometer (AAS, SpectrAA 300, Varian Inc., Darmstadt, Germany) at standard operating conditions.

We also collected 12 water samples from tanks of varying size (26–100 cm longest leaf length) of the population in Bocas del Toro in the late dry season and determined their Cl^- concentrations with an HPLC (Dionex 4500i with pulsed amperometric detection, Dionex, Sunnyvale, CA, USA). For 32 additional plants in Bocas del Toro (range 5–111 cm longest leaf) and 27 plants from Barro Colorado Island (range 6–87 cm longest leaf) we determined leaf thickness in the upper half with a calliper to the nearest 0.01 mm.

Germination experiment

Seeds of various parent plants were germinated in Petri dishes on moist filter paper in a growth cabinet (Economic Delux, Snijder Scientific, Tilburg, the Netherlands). Air temperature was 25°C, and photon flux density (PFD) at the level of the seeds was c. $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a day/night regime of 12 h/12 h. For each of three provenances (Bocas del Toro, BCI and Fortuna), five Petri dishes with 20 seeds each were assigned to each of four sea water concentrations and a control. Seeds were rinsed daily with 10 ml of different solutions prepared from distilled water and sterilized sea water obtained off-shore in the North Sea (5%, 10%, 15%, 50% sea water) and with distilled water (= controls). Germination (= emergence of the hypocotyl) was recorded daily for up to 30 d.

Seedling experiment

Seeds were allowed to germinate under conditions resembling those of the controls of the preceding germination experiment. After reaching a size of c. 0.6 cm (average plant dry weight $3.4 \pm 0.4 \text{ mg}$, $n = 36$), the atmospheric seedlings were assigned to different treatments and a control. During the entire duration of the experiment (10 wk), plants were kept in Petri dishes on moist filter paper in the same growth cabinets as described above with similar light and temperature conditions. For each of three provenances (Bocas del Toro, BCI and Fortuna), five Petri dishes with 10 seedlings each were assigned to each of five sea water concentrations and a control. Plants were rinsed every 2–3 d with 750 μl of solutions of one of five different sea water concentrations (2.5%, 5%, 15%, 30%, 50%) and with

distilled water (= controls). Mortality was checked daily. At the beginning and end of the experiment, plant fresh weight was determined. Initial plant dry weight, which was used to determine RGR, was estimated from fresh weight using a water content of 78% determined from 10 replications (SD = 2%).

Growth experiments and sodium and potassium accumulation

A first growth experiment, which lasted for 4 wk, was conducted in a climate chamber (Microclima 1750E, Snijder Scientific, Tilburg, the Netherlands) under the following conditions: PFD: $220 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 12 h, air temperature: 25°C , day; 15°C , night; relative air humidity: 60%, day; 85%, night; external CO_2 concentration *c.* $370 \mu\text{l l}^{-1}$. All plants had developed a tank from overlapping leaf bases, which was refilled daily with different solutions prepared from distilled water and sterilized sea water obtained off-shore in the North Sea (2.5%, 5%, 10%, 15%, 30%, 50% sea water and controls). Once per week all tanks were rinsed with distilled water to avoid accumulation of solutes, and then refilled with diluted fertilizer solution (Flory 3: 15–10–15, Eufloor, Munich, Germany) for the remaining day. The response variable in this growth experiment was relative growth rate (RGR, in $\text{mg g}^{-1} \text{d}^{-1}$), defined as (Evans 1972):

$$\text{RGR} = (\ln \text{DW}_{\text{final}} - \ln \text{DW}_{\text{initial}}) / \Delta t \quad (1)$$

in which DW is plant dry weight and Δt is the duration of the experiment in days. The initial DW was estimated from the measured fresh weight using the average ratio of FW and DW, the final DW was directly determined gravimetrically.

In a second experiment we determined the accumulation of Na and changes of K as a function of the sea water concentration in the tank fluids after 8 wk. Growth conditions were identical to the 4-wk growth experiment. After the final harvest, Na and K concentrations were determined with an AAS as described above. To determine possible damage before visible cues were noticeable, the maximum apparent quantum yield (F_v/F_m , compare Lambers *et al.* 1998) was determined with dark-adapted plants (30 min darkness) of the different treatment levels and the control (distilled water) before and during the experiment with a Mini-PAM (Walz, Effeltrich, Germany).

Based on the results of the two preceding experiments, a third experiment, which lasted for 12 wk, combined the analysis of both relative growth rates and Na accumulation and changes in K concentrations. Experimental conditions and details of determination of

Table 1. Concentrations of sodium and potassium in plants from four different populations of *Werauhia sanguinolenta* in $\text{mg nutrient element g DW}^{-1}$. Data are mean \pm SD, $n = 4$. Different letters within a column indicate significant differences (ANOVA, Tukey HSD test $P < 0.05$).

Population	Habitat	Na	K
Bocas del Toro	Coastal forest	17.8 ± 2.3^a	17.5 ± 4.0^b
BCI	Lowland seasonal forest	2.3 ± 0.1^b	20.2 ± 1.6^{ab}
Fortuna	Lower montane rain forest	3.6 ± 0.1^b	27.7 ± 1.7^a
Veraguas	Secondary vegetation	2.4 ± 0.5^b	23.2 ± 6.6^{ab}

RGR, apparent quantum yield, and Na and K concentrations were as described above.

Data analysis

Data were analysed with R 2.6.2 (<http://www.R-project.org>). Germination data were arcsine square root-transformed before analysis. Normal distribution and homoscedasticity were checked when applicable. All error terms are standard deviations.

RESULTS

In situ morphology and Na^+/K^+ concentrations

Plants growing close to the sea shore in Bocas del Toro did not develop thicker leaves than those from the inland population in BCI. Leaf thickness ranged from 0.21 mm in the smallest tanks to 0.95 mm in the largest, but the regression lines for both sites were virtually identical (BCI: Leaf thickness (mm) = $0.0057 \text{ LL} + 0.25$, $n = 27$, $r^2 = 0.92$, Bocas del Toro: Leaf thickness (mm) = $0.0063x + 0.20$, $n = 32$, $r^2 = 0.84$). On the other hand, the Na^+ concentration of small plants from Bocas del Toro was significantly higher than that of conspecifics from the three inland populations, while the K^+ concentrations in this population tended to be lowest (Table 1). An analysis of the Cl^- concentrations of fluid from tanks from Bocas del Toro ranging in size from 26–110 cm (maximal leaf length) yielded values between 0.4–11.6 mmol l^{-1} , which is equivalent to *c.* 0.1–2% sea water.

Germination

Overall, seeds from plants from Bocas del Toro showed slightly poorer germination compared to those from BCI and Fortuna, but did not differ from the two inland populations in their sensitivity to salinity (Table 2). Invariably, external concentrations (C_{ext}) of 0–15% sea water ($\leq 0.5\%$ NaCl) caused no reduction in the proportion of germinated seeds (Tukey HSD test, $P > 0.05$), while germination largely failed at 50% sea water (*c.* 1.75% NaCl).

Table 2. Changes in the germination success (%) with increasing external salt concentration (C_{ext} , in % sea water) in three populations of *Weruuhia sanguinolenta* (coastal population: 'Bocas'). Data are mean \pm SD, $n = 5$ batches of 20 seeds.

C_{ext}	Bocas	BCI	Fortuna
0%	91 \pm 7	87 \pm 15	99 \pm 3
5%	85 \pm 11	95 \pm 4	94 \pm 8
10%	83 \pm 8	100 \pm 0	98 \pm 4
15%	88 \pm 14	84 \pm 24	96 \pm 4
50%	13 \pm 7	30 \pm 26	0 \pm 0

Growth and survival of seedlings

Seedling growth and survival was affected by slightly lower salt concentrations than germination, but again there was no evidence for higher tolerance of individuals from Bocas del Toro to sea water (Figure 1). Plants from all three populations showed a trend towards slower growth with increasing C_{ext} , RGR at a C_{ext} of 15% sea water (c. 0.5% NaCl) being only half the maximum rate. The same concentration had hardly any effect on either germination or seedling mortality (Table 2, Figure 1). In all three populations, there was a steep increase in

mortality at $C_{ext} \geq 30\%$ sea water (c. 1% NaCl), with very few plants surviving 10 wk of exposure to C_{ext} of 50% sea water (c. 1.75% NaCl).

Growth, survival and Na accumulation of juveniles

Both population and salinity had a significant effect on growth measured over 4 wk (Table 3, Figure 2). Plants from the Fortuna and Veraguas populations grew significantly faster than those from Bocas del Toro and BCI (two-way ANOVA, Tukey HSD test $P < 0.05$). The growth response to salt, however, was not modulated by population (two-way ANOVA, interaction term: population $\times C_{ext}$: $P = 0.73$): invariably, growth reached maximum values at C_{ext} of 2.5–15% sea water, while higher concentrations had dramatic effects. After 1 wk, plants looked invariably healthy, but apparent quantum yield was reduced at the highest salt levels, i.e. to $60\% \pm 4\%$ ($n = 16$, 30% sea water) or only $35\% \pm 7\%$ ($n = 16$, 50% sea water) of initial values ($F_v/F_m = 0.80 \pm 0.01$, $n = 32$). No change in F_v/F_m was observed at other concentrations. Prolonged exposure led

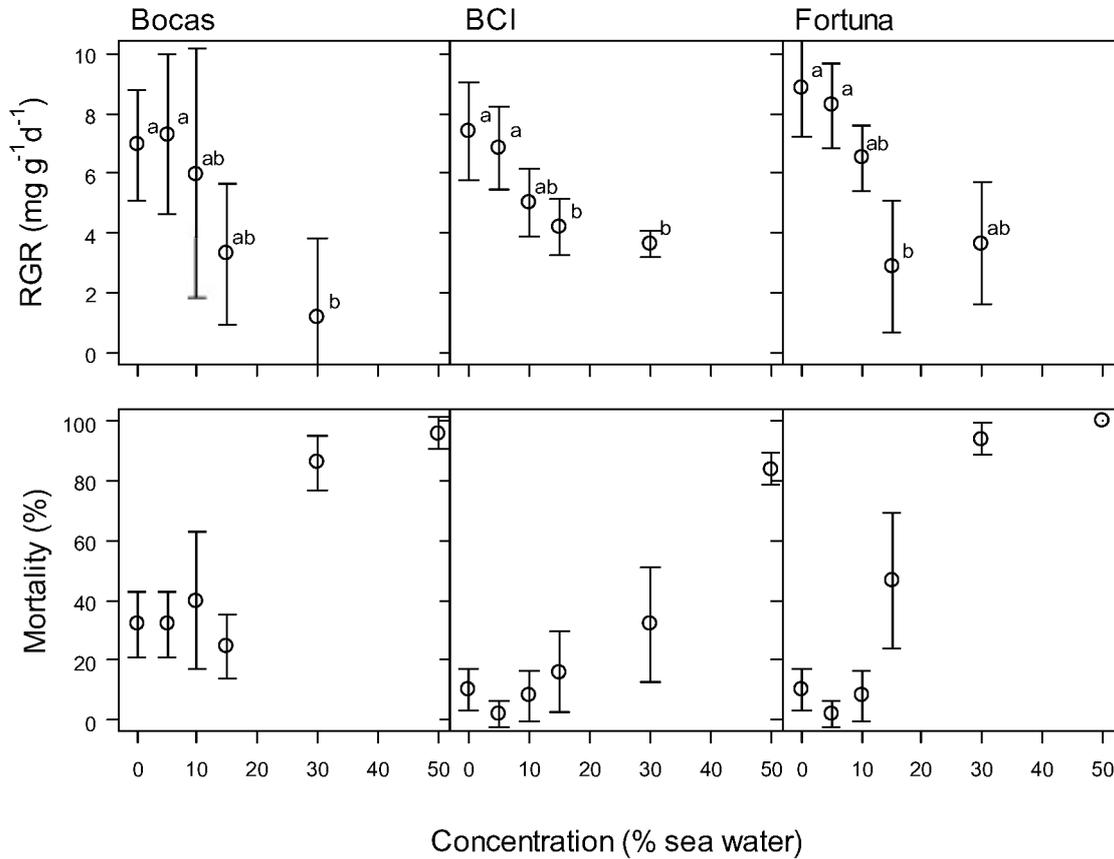


Figure 1. Relationships of relative growth rates and mortality to increasing external salt concentrations in seedlings from three populations of *Weruuhia sanguinolenta* over a period of 10 wk (coastal population: 'Bocas'). Data are mean \pm SD, $n = 5$ batches of initially 10 seedlings. Different letters indicate significant differences (ANOVA, Tukey HSD, $P < 0.05$).

Table 3. Results of a two-way ANOVA of the effects of external salt concentration (C_{ext}) and population on relative growth rate (RGR). Given are degrees of freedom (df), sum of squares, F-values, and significance levels (P).

Factor	df	F value	P
C_{ext}	6	3.38	0.005
Population (P)	3	4.80	0.004
$P \times C_{\text{ext}}$	18	0.77	0.73
Residuals	84		

to visible signs of damage (necrosis) in the plants with the highest C_{ext} . After 4 wk, all but two plants with C_{ext} of 50% sea water had died. In plants receiving 30% sea water, only three plants (*c.* 20% of the total) died during the same time, but RGRs tended to decline, although their apparent quantum yield showed no further decrease ($64\% \pm 13\%$ of initial values, $n = 13$).

In a second experiment, there was considerable mortality in plants treated with 20–25% sea water after 8-wk exposure with no losses among plants receiving lower concentrations (data not shown). Again, plants from Bocas del Toro were neither particularly tolerant nor particularly susceptible: mortality was highest in plants from BCI with, respectively, 75% and 100%, and lowest in plants from Fortuna with, respectively, 25% and 0%. After 12 wk (experiment 3) visible signs of damage were observed at much lower C_{ext} . This coincided with reduced F_v/F_m ratios and reduced growth rates: the apparent quantum yields were just 69% (15% sea water) and 89% (10% sea water) of those obtained in plants with lower salt concentrations in their tanks (average $F_v/F_m = 0.82 \pm 0.01$, $n = 16$), and RGR was frequently negative in plants with tank fluids of 15% sea water (Figure 3). Both population and C_{ext} had significant effects on RGR (two-way ANOVA, $P < 0.05$), but the interaction

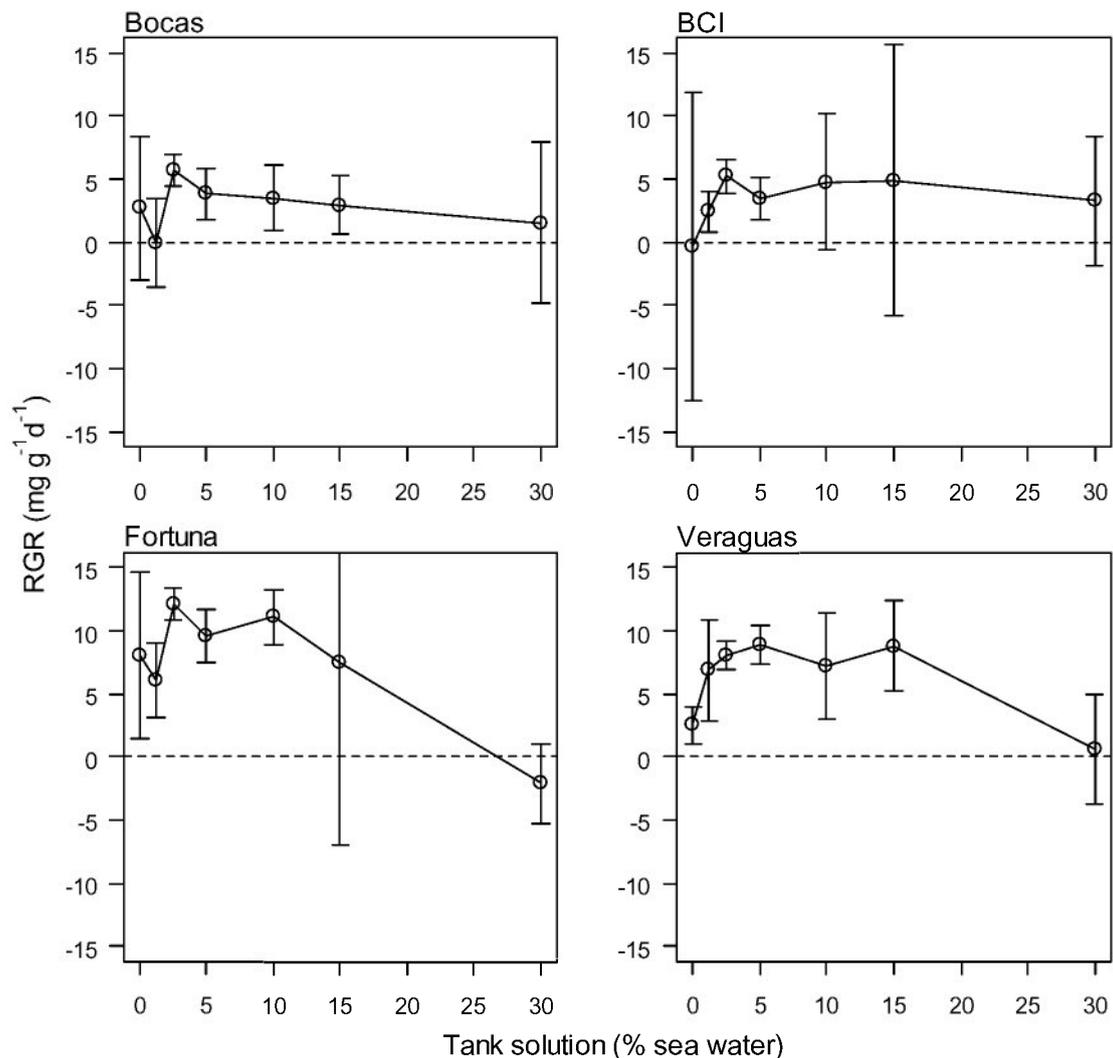


Figure 2. Relationship between relative growth rate and salt concentration in the tank (C_{ext}) in juveniles from four populations of *Werauhia sanguinolenta* after 4 wk (coastal population: 'Bocas'). Data are mean \pm SD, $n = 4$ plants.

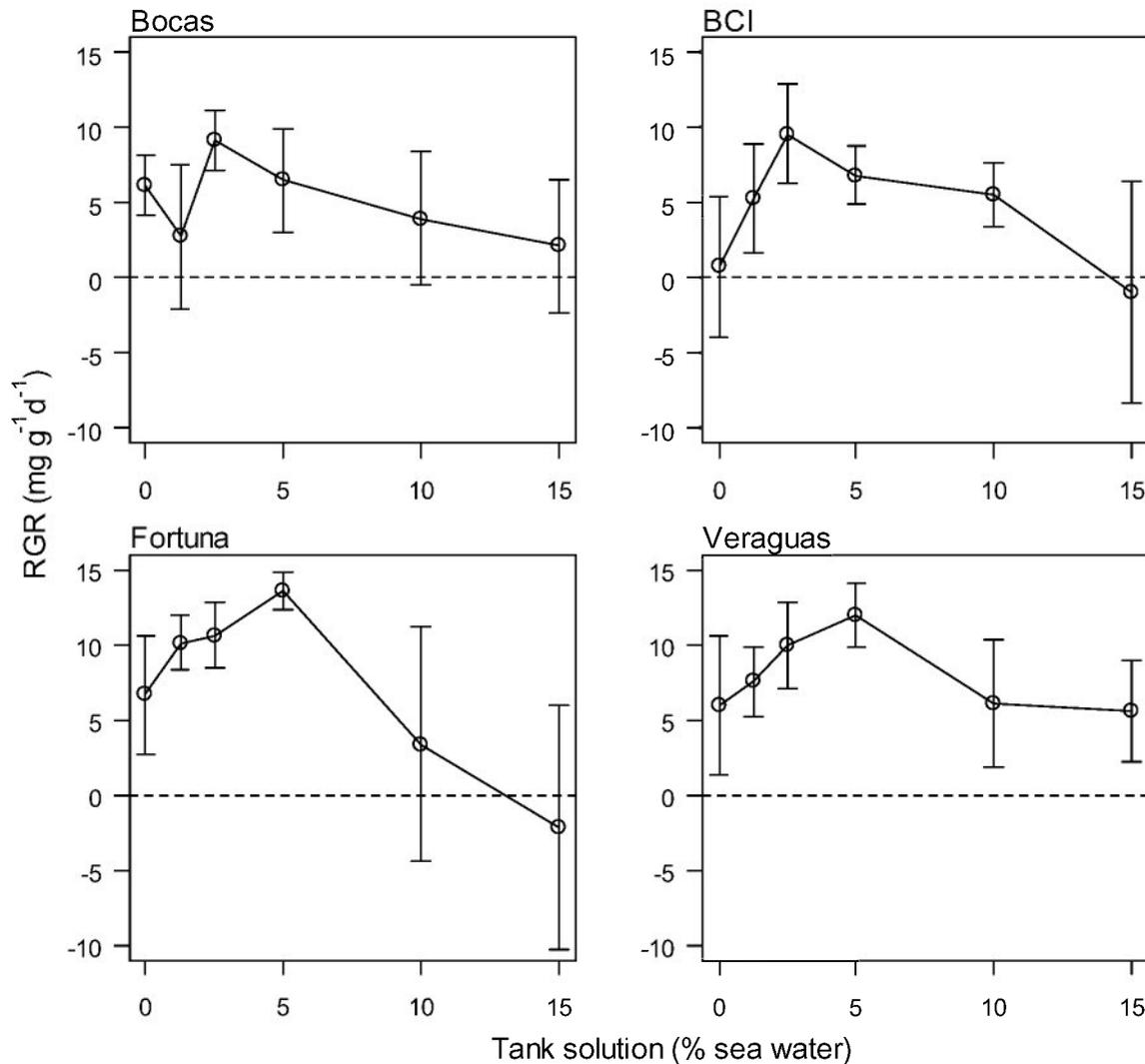


Figure 3. Relationship between relative growth rate and salt concentration in the tank fluid (C_{ext}) in juveniles from four populations of *Weruuhia sanguinolenta* after 12 wk (coastal population: 'Bocas'). Data are mean \pm SD, $n = 4$ plants.

term was not significant ($P = 0.17$). No mortality was observed but plants receiving 10% and 15% sea water showed signs of stress (necrotic outer leaves).

Expressed on a dry weight basis Na^+ concentrations in tissues $[\text{Na}^+]$ after 8 wk showed a saturation-like increase with higher C_{ext} (Figure 4). Notably, the maximum $[\text{Na}^+]$ exceeded $50 \text{ mg Na}^+ \text{ gDW}^{-1}$ at C_{ext} of 25% sea water. The calculated $[\text{Na}^+]$ in the leaf-sap increased much faster than dry-weight based Na^+ between 20% and 25% sea water, which can be explained by sharply decreasing plant water contents (data not shown). Longer exposure to salt concentrations for 12 wk led to significant increases in $[\text{Na}^+]$ only at higher C_{ext} ($\geq 5\%$ sea water; Table 4, three-way ANOVA, Tukey HSD on the interaction term salt water level \times time, $P < 0.05$). For example, in plants receiving tank fills of 15% sea water $[\text{Na}^+]$

increased from $40 \pm 11 \text{ mg Na}^+ \text{ gDW}^{-1}$ after 8 wk to $53 \pm 7 \text{ mg Na}^+ \text{ gDW}^{-1}$ after 12 wk. These figures allow an estimation of the critical $[\text{Na}^+]$ causing mortality. After 8 wk, tissue concentrations of $c. 50 \text{ mg Na}^+ \text{ gDW}^{-1}$, reached at C_{ext} of $c. 20\text{--}25\%$ sea water, were associated with visual damage and increased mortality (Figure 4). Similar $[\text{Na}^+]$ were observed after 12 wk exposure to lower C_{ext} ($c. 15\%$ sea water) with similar symptoms (Figure 3) and may thus constitute the tolerance limits for tissue concentrations in *W. sanguinolenta*.

Concentrations of K in tissues ($[\text{K}^+]$) were also significantly affected by C_{ext} , population and time (Table 4) with a positive relationship of C_{ext} and $[\text{K}^+]$ and a negative relationship of time and $[\text{K}^+]$. Consistent with the original differences among populations (Table 1), plants from Fortuna had the highest $[\text{K}^+]$ (Tukey HSD, $P < 0.05$).

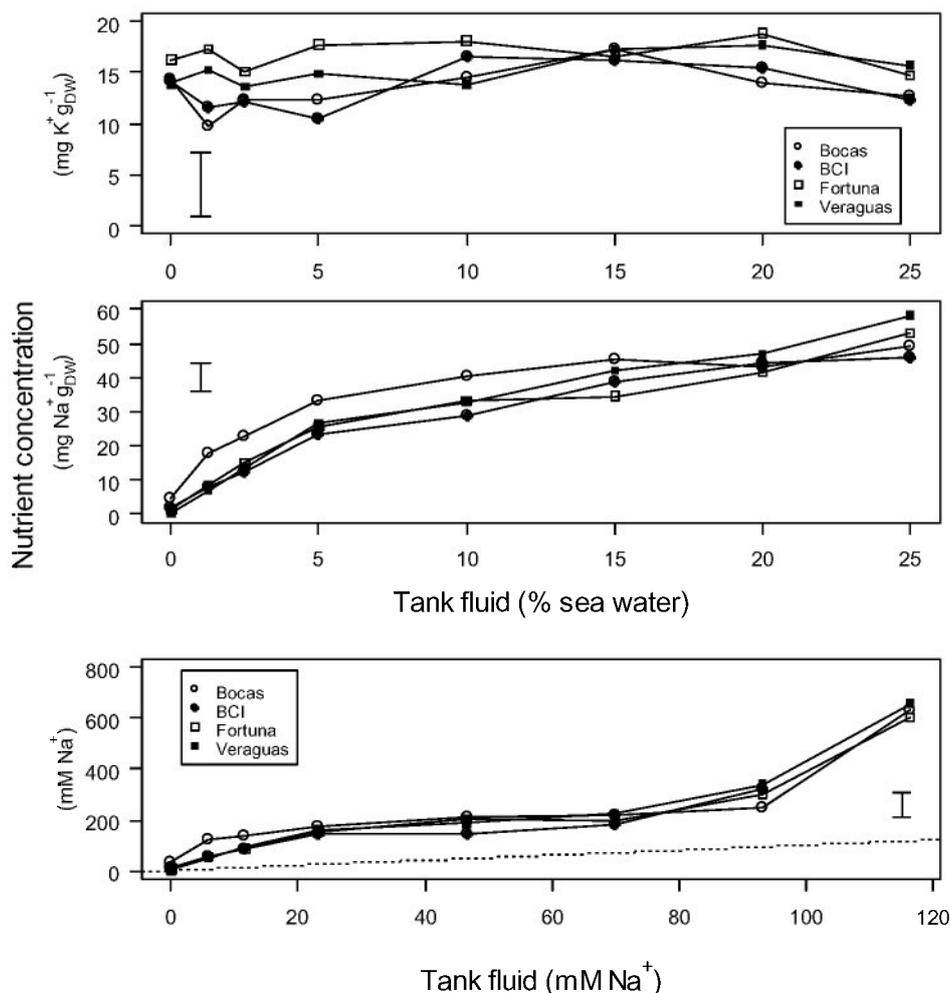


Figure 4. Na⁺ and K⁺ concentrations as a function of salt concentration in the tank (C_{ext}) in juveniles from four populations of *Werauhia sanguinolenta* after 8 wk (coastal population: 'Bocas'). Concentrations are expressed on a dry-weight basis (a, b) or as calculated leaf-sap concentrations (c) using plant water content. Data are means. For clarity, only the average SD is shown in each plot instead of individual SDs; $n = 4$ plants, although mortality in the two highest tank solutions reduced sample sizes in most cases. In one extreme case ('BCI', 25% sea water) the K⁺ and Na⁺ concentrations represents values of dead plants. The dotted line (c) indicates the 1:1 relationship of internal and external concentrations.

DISCUSSION

Halophytes are normally distinguished from glycophytes as those plants that are able to complete their life cycle in high salt environments, which are defined by salt concentrations exceeding 0.5% or about 85 mM NaCl (Watkins *et al.* 1988). Indeed, there are terrestrial members of the Bromeliaceae such as *Pitcairnia halophila* that fulfil this definition (Benzing 2000). Remarkably, the epiphytic bromeliad species we studied was able to germinate and also to grow and survive for at least 2 mo under such saline conditions. However, after longer exposure (12 wk) growth rates with tank fluids equivalent to 0.5% NaCl tended to be close to zero or negative, which makes successful completion of the life cycle under saline conditions not very likely. On the other hand, additions of more diluted sea water to the tank tended

to have a positive effect on growth in juveniles compared with controls, which suggests that *W. sanguinolenta* can be categorized as a relatively salt-tolerant glycophyte (*sensu* Greenway & Munns 1980). This interpretation also takes into account (1) the observation that both Na⁺ and K⁺ were positively correlated with external salt concentrations, which is typical for more salt-sensitive species (Greenway & Munns 1980), as well as (2) the remarkably high Na⁺ concentrations found in living tissue (up to *c.* 50 mg Na⁺ g_{DW}⁻¹), which resemble those found in many halophytes (Ungar 1991). Similarly high concentrations of sodium on a dry weight basis have been reported previously for other epiphytic bromeliads (Benzing & Renfrow 1971, 1974; Shacklette & Connor 1973), but expressed as ionic concentration in leaf-sap our values of undamaged plants (> 200 mM Na⁺ kg⁻¹) are considerably higher than available data (*Tillandsia*

Table 4. Results of two three-way ANOVAs of the effects of salt concentration in tank fluid (C_{ext} : 0–15% sea water), duration of the experiment (8 wk vs. 12 wk) and population on tissue concentrations of Na and K. Given are degrees of freedom (df), F-values, and significance levels (P).

Factor	df	F value	P
Na			
C_{ext}	5	6.5	< 0.001
Population (P)	3	10.2	< 0.001
Time (T)	1	0.7	0.37
$C_{\text{ext}} \times P$	15	1.1	0.32
$C_{\text{ext}} \times T$	5	3.5	0.004
$P \times T$	3	1.6	0.17
Residuals	159		
K			
C_{ext}	5	6.5	< 0.001
Population (P)	3	6.9	< 0.001
Time (T)	1	5.1	0.02
$C_{\text{ext}} \times P$	15	0.6	0.86
$C_{\text{ext}} \times T$	5	0.7	0.62
$P \times T$	3	2.1	0.10
Residuals	159		

flexuosa (Bromeliaceae): 137 mmol kg⁻¹; *Schomburgkia humboldtiana* (Orchidaceae): 149 mmol kg⁻¹; Griffiths *et al.* 1989). Tissue concentrations of Na⁺ exceeded by far external concentrations. It is known that Na⁺ can use the low-affinity transport systems for K, which is rather unspecific (Subbarao *et al.* 2003) to enter the cytosol, from where it may pass the tonoplast and be concentrated substantially in the vacuole. Some glycophytes are able to excrete Na⁺ from roots, exclude it from the xylem, or transport it back to the roots via the phloem (Lambers *et al.* 1998), but such options seem not possible in plants that take up water and nutrient with their leaves. As pointed out by Benzing (2000) there is an urgent need to understand trichome function in this context.

Is *W. sanguinolenta* growing close to the surf potentially threatened by excessive salt input? Our data provide no indication that this is the case in our study population: (1) determinations of the actual salt concentrations in tank fluids in the natural setting yielded low values. Since these samples were taken in the dry season, when concentrations are expected to be highest, this suggests that critical values are unlikely to be reached at our study site in Bocas del Toro; (2) tissue concentrations of Na⁺ were only slightly elevated compared with plants growing inland (Table 1); (3) no increase in leaf thickness was detected, which is a frequently observed consequence of growth under more saline growth conditions (Watkins *et al.* 1988). As suggested previously, a moderate input of salt spray may even be beneficial for epiphytic growth (Benzing 2000), which matches the visual impression of lush epiphytic vegetation at this and other sites along the Caribbean coast of Panama (Zotz, pers. obs.). It has been argued repeatedly (Benzing 2000, Subbarao *et al.*

2003) that Na may be able to replace K and other nutrient elements functionally when these cations are scarce. The positive relationship of external salt concentration and RGR in the lower range of C_{ext} in our experiments are certainly consistent with this notion.

Not surprisingly then, we did not find any indication for physiological and demographic parameters related to salt tolerance in the population growing close to the sea to be different from those from inland sites, neither germination response, growth and mortality of seedlings, nor growth, mortality and changes of sodium and potassium concentration in small plants. Still, some population differences were detectable. For example, individuals from Fortuna and Veraguas grew generally faster and tended to have higher tissue concentrations of K, but we cannot offer an ecological interpretation for these observations.

There is the general notion that earlier life stages should be more vulnerable to high salinity (Ungar 1991). However, germination and growth of seedlings of *W. sanguinolenta* were not more affected by salinity than growth of larger plants when compared for similar periods of time (8–10 wk). Indications of damage became obvious when external solutions exceeded *c.* 15% of sea water concentration, which is equivalent to *c.* 0.5% Na or *c.* 75 mmol Na⁺ kg⁻¹. Growth in seedlings seems to be affected by somewhat lower C_{ext} than growth of juveniles, but considerable variation and relatively low sample size precludes a finer-scale identification of possible differences.

In summary, consistent with the few reports for epiphytes to date *W. sanguinolenta* can tolerate surprisingly high tissue concentrations of sodium, but lacks the characteristics of a true halophyte. However, our data suggest significant uptake of sodium. Since exclusion of Na⁺ is apparently lacking, critical tissue concentrations may result from long-term exposure to small or moderate external sodium concentrations. Thus, high precipitation which dilutes potentially harmful input by salt spray may still be an essential prerequisite to allow the abundant occurrence or epiphytes in coastal forests in the tropics (Gómez & Winkler 1991).

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