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Photosynthetic responses to submergence in mangrove seedlings

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Abstract. Flooding and salinity fluctuations are common in mangrove systems. Sometimes these events are long-lasting, persisting several months. With an increased frequency of heavy rainfalls and terrestrial run-off, subsequent floods have been associated with massive mangrove mortality and failure to regenerate in the region. Owing to climate change, these events are expected to be more common in the future. We investigated how three weeks of submergence in water of different salinities affected the photosynthetic rates in seedlings of three common mangroves: *Bruguiera gymnorrhiza* (L.) Lamk.; *Avicennia marina* (Forssk.) Vierh.; and *Heritiera littoralis* Dryand. We found that photosynthesis and survival rates declined with increasing salinity and submergence time for all species. Prolonged submergence caused a significant decline in photosynthetic rates (as electron transport rate – ETR) for *B. gymnorrhiza* ($P = 0.021$) and *H. littoralis* ($P = 0.002$), whereas significant effects of both salinity ($P = 0.003$) and submergence ($P = 0.023$) were observed between species. Maximum diurnal values of ETR declined in the order of *A. marina* > *B. gymnorrhiza* > *H. littoralis*. After submergence, survived seedlings were tended normally, watered twice a day with freshwater. Three seedlings of *B. gymnorrhiza* from freshwater and 33% seawater treatments and of *A. marina* from freshwater treatment displayed signs of recovery for the first 3–5 days, but after that they died. We conclude that submergence time and water salinity will affect the performance of mangrove areas, such that areas experiencing prolonged submergence with flooding dominated by saline water might be most severely impacted.

Additional keywords: flooding, Fv/Fm, mangrove seedlings, photosynthesis, salinity, underwater.

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Introduction

Mangroves occur in the intertidal zones of tropical and sub-tropical regions where they frequently experience regular tidal inundation of varying salinities. In view of current climate change predictions, these areas will likely face challenges of increased flooding from increased precipitation and global sea-level rise (Ellison and Farnsworth 1997; Naidoo *et al.* 1997). Mangrove plants, especially seedlings not yet strong enough to withstand environmental shocks, are most vulnerable to degradation. In extreme flooding situations with prolonged submergence of the whole plant, the ability of the plant to respond to the stresses of submergence becomes crucial for its survival (Vervuren *et al.* 2003). Mangroves, however, are not known to be very tolerant of underwater stress; flooding might therefore be stressful for smaller mangrove seedlings because they would then experience whole-plant submergence, thus facing reduced gaseous exchange and depressed light intensity (Ashford and Allaway 1995). Salinity has also been reported to compound the effect of inundation on the physiological tolerance of mangrove seedlings (Krauss and Allen 2003; Ye *et al.* 2003, 2005). In tropical river estuaries, where flooding events and submergence may last days, weeks, and even months, complete submergence can directly influence photosynthetic functions while the shoots remain under water (Erftemeijer and Hamerlynck 2005; Barbosa *et al.* 2001; Wieczkowski 2009).

Effects of waterlogging on mangrove seedling growth and photosynthesis have been reported (Ellison and Farnsworth 1997; Ye *et al.* 2003; Luzhen *et al.* 2005; Krauss *et al.* 2008). However, to our present knowledge there has been no reported work examining whether and how photosynthesis continues underwater in mangrove seedlings exposed to both extended periods of high water, as well as different levels of seawater–river water mixtures. An experiment conducted by Luzhen *et al.* (2005) involved periodic submergence of seedlings of the mangrove *Kandelia candel* L., but photosynthetic measurements were made only after draining the artificial tidal tanks to expose the shoots. For wetland plants other than mangroves, for example, there is considerable inherent variation between species in tolerance to underwater stress (Vervuren *et al.* 1999; Mommer and Visser 2005). Pezeshki *et al.* (1987) argued that the survival and growth of a given species when exposed to underwater stress conditions depend on its ability to maintain a

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functional photochemical and biochemical system that enables maintenance of positive net photosynthesis. We set up a mesocosm experiment to investigate whether photosynthesis in mangrove seedlings of *B. gymnorrhiza*, *A. marina*, and *H. littoralis* continues underwater and how the species differ in tolerance.

Materials and methods

Plant and soil materials

Mature and freshly shed propagules of *B. gymnorrhiza* and seeds of *A. marina* and *H. littoralis* were collected from Ruvu Estuary mangrove stands, north of Bagamoyo (6°22′S–6°27′S), Tanzania. They were transported to the experimental site at Buyu, situated beside a mangrove stand about 15 km south of Zanzibar town. This experimental site experiences weather conditions similar to those of Ruvu Estuary, i.e., it is hot and humid throughout much of the year with an average annual temperature of 28°C and over 1000 mm of annual precipitation falling in a bimodal pattern.

Plant materials were sorted and propagules and seeds of approximately the same size and weight were selected for seedling production in an open-air nursery, shaded with transparent roofing sheets that allowed light intensities of 250–400 μmol photon m^{-2} s^{-1} of natural sunlight to penetrate. Propagules of *B. gymnorrhiza* were planted individually in small plastic pots (10 cm diameter × 15 cm height) while seeds of *A. marina* and *H. littoralis* were sown in a sand bed using a 3 : 1 mixture of forest soil (collected from the same mangrove sites as the propagules and seeds) and washed beach sand. The pots were watered twice a day using freshwater from a nearby natural well. When the seedlings reached three fully expanded leaf pairs, they were transplanted into plastic buckets (25 cm diameter × 30 cm height) filled halfway with the same soil mixture and allowed to grow until they were six months old. Every four weeks, the top half of the potting soil mixture in the buckets was carefully removed with minimal disturbance to the roots and replaced with fresh potting soil to minimize nutrient limitations.

Experimental treatments

Main experiment

White transparent plastic tanks (100 cm diameter × 110 cm height) of approximately 860 L capacity were used for the submergence experiment. A drainage hole was made in the base of each tank and sealed with a rubber stopper. For each of the three species, four submergence treatments were applied using salinity levels of 0%, 33%, 66%, and 100% seawater obtained by mixing natural seawater of a salinity of 35 with freshwater in proportions of 0 : 100, 33 : 66, 66 : 33, and 100 : 0 seawater : freshwater, respectively. Three replicates were made of each salinity treatment to assess whether photosynthesis continued underwater and whether there was variation between species in this regard.

All tanks were placed in open sunlight, and five potted seedlings of each species were placed in a tank for each salinity treatment. Tanks were slowly filled with the appropriate water media until all seedlings' apical buds were 25–30 cm under water. Light intensity in terms of photosynthetic active radiation (PAR) at this depth was 35–50% of the light at the surface, which was maximally 1400–1600 μmol photon m^{-2} s^{-1}; submergence was then maintained for 21 days. Salinity was checked daily and regulated by adding either freshwater or seawater to maintain the levels. Each tank was carefully and gently stirred manually at least twice a day to make sure that water media did not become stagnant and water temperature remained close to ambient temperature, averaging 24°C. A set of five additional seedlings of each species was planted in containers (using same soil mixture) beside the treatment tanks to serve as control plants. These were maintained by watering with freshwater twice a day throughout the experiment. At the end of underwater treatments, tanks were slowly drained by releasing the rubber stopper at the base, and any surviving seedlings were removed. Seedlings were considered to have survived if they still had green stems, signs of new sprouts, and intact leaves that still produced a detectable fluorescence signal. After submergence, surviving seedlings were watered with normal freshwater twice a day to monitor their recovery from submergence stress.

pH drift experiment

A short-term pH drift experiment was performed in the laboratory with fresh leaf blades of *B. gymnorrhiza* incubated in water. Five leaf blades each were put in 300-mL clear glass Erlenmeyer flasks sealed with air-tight caps. Two sets of six bottles, each containing five leaf blades, were filled with freshwater and another two sets were filled with seawater. To each set, one filled bottle without leaves was added as a control. One set of bottles for each water medium was placed in light, which, on average, increased from 500 to 1400 μmol photon $m^{-2}s^{-1}$, and another in darkness for two hours from 08 : 00 to 10 : 00 local time. The pH of the water medium was measured in each bottle every 30 min to determine whether CO_2 exchange between the leaves and the surrounding medium continued underwater. Measuring pH change, which reflects the sum of photosynthetic uptake and respiratory release of CO_2 in the light, and only the respiratory release of CO_2 in the dark, is an accepted technique for estimating the uptake of CO_2 from water by a plant (e.g. Axelsson 1988).

Photosynthesis measurements

The first photosynthesis measurements were made after 24 hours of submergence and then repeated after 7, 14, and 21 days using chlorophyll fluorescence (Diving-PAM Underwater Chlorophyll Fluorometer; Heinz Walz GmbH, Effeltrich, Germany). Point measurements of photochemical yield (Y), photosynthetic electron transport rate (ETR), and corresponding PAR were made as described by Beer *et al.* (2001), whereby the main optical fibre of the instrument was held approximately 10 mm from the leaf surface using a leaf distance clip. The quantum sensor was affixed to the leaf-distance clip and positioned in such a way that, during measurement, it remained perpendicular to the incident light.

Measurements were made on five leaf blades from the second and third fully expanded apical leaf pairs of each surviving seedling every two hours from 04 : 00 to 20 : 00 hours. Yield measurements between 04 : 00 and 06 : 00 in the morning and 18 : 00 and 20 : 00 in the evening represented the dark-adapted maximum variable fluorescence (Fv/Fm). Computed mean

Table 1. Results of pH drift experiment on *B. gymnorrhiza* (mean ± s.e., $n = 6$) to validate whether photosynthetic carbon fixation progresses under water in different salinities

Treatment		Time					Control	*F*	*F crit*	*P*
		08 : 00	08 : 30	09 : 00	09 : 30	10 : 00				
Light	Freshwater	7.55 ± 0.001	7.64 ± 0.01	7.79 ± 0.04	7.87 ± 0.05	8.06 ± 0.05	7.51 ± 0.01	2.555	2.54	0.048
	Seawater	8.21 ± 0.00	8.23 ± 0.003	8.26 ± 0.01	8.29 ± 0.01	8.32 ± 0.01	8.21 ± 0.003			
Dark	Freshwater	7.54 ± 0.002	7.49 ± 0.01	7.45 ± 0.01	7.43 ± 0.01	7.38 ± 0.02	7.51 ± 0.01	0.083	2.54	0.987
	Seawater	8.21 ± 0.00	8.19 ± 0.003	8.18 ± 0.003	8.17 ± 0.003	8.21 ± 0.15	8.22 ± 0.003			

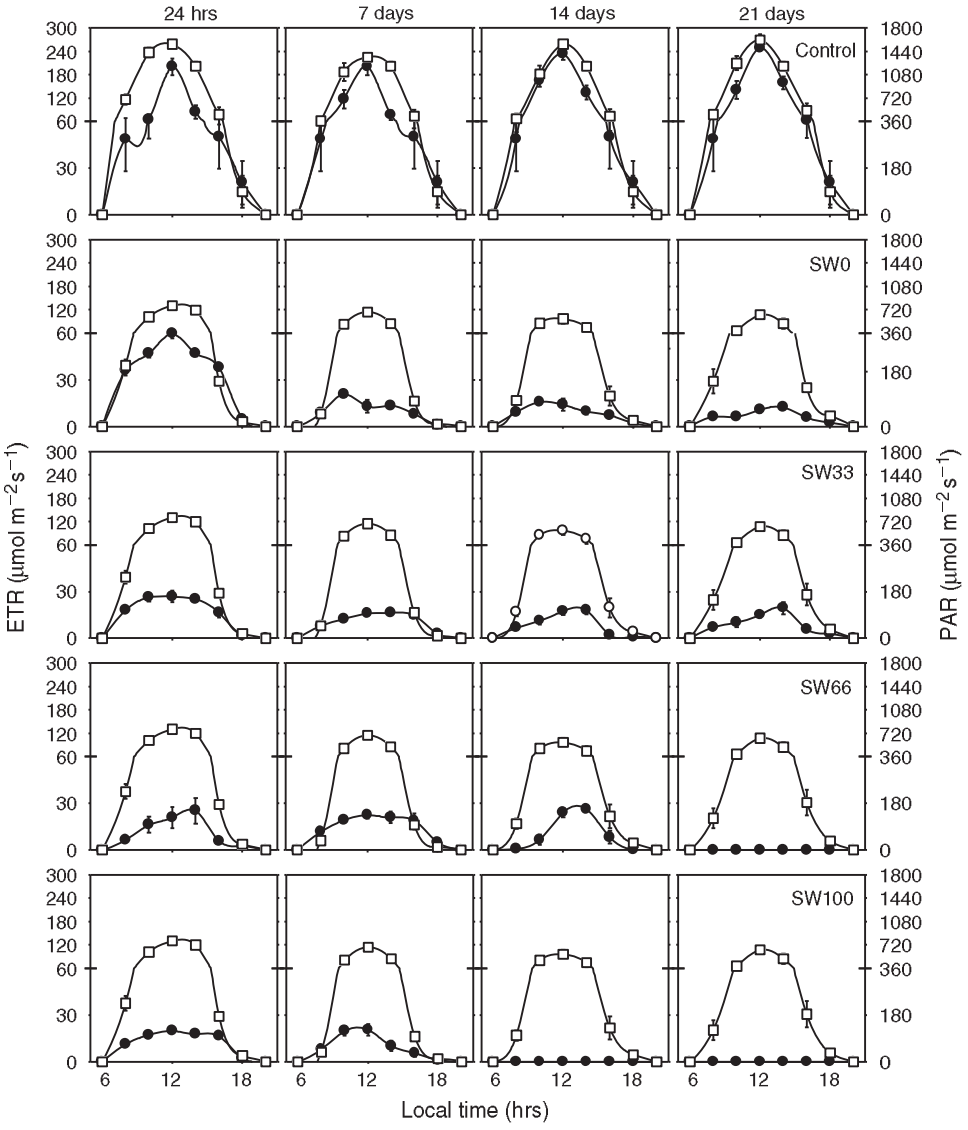


Fig. 1. Underwater response curves of photosynthetic electron transfer rate (ETR; ●) as a function of photosynthetic active radiation (PAR; □) for *B. gymnorrhiza* seedlings in different salinities over a duration of 21 days of submergence (means ± 1 s.d., $n = 15$).

values of photosynthetic measurements were checked for normality and homogeneity of variance, transformed where necessary, and used for graphical presentations and statistical analysis of variance (ANOVA) with *F*-tests at $P \leq 0.05$ using SigmaPlot 8.0 (SPSS Inc., Chicago, IL, USA) for Windows XP to examine the individual and interactive treatment effects. The experiment had two main effects (underwater, salinity), and one sub-effect (species).

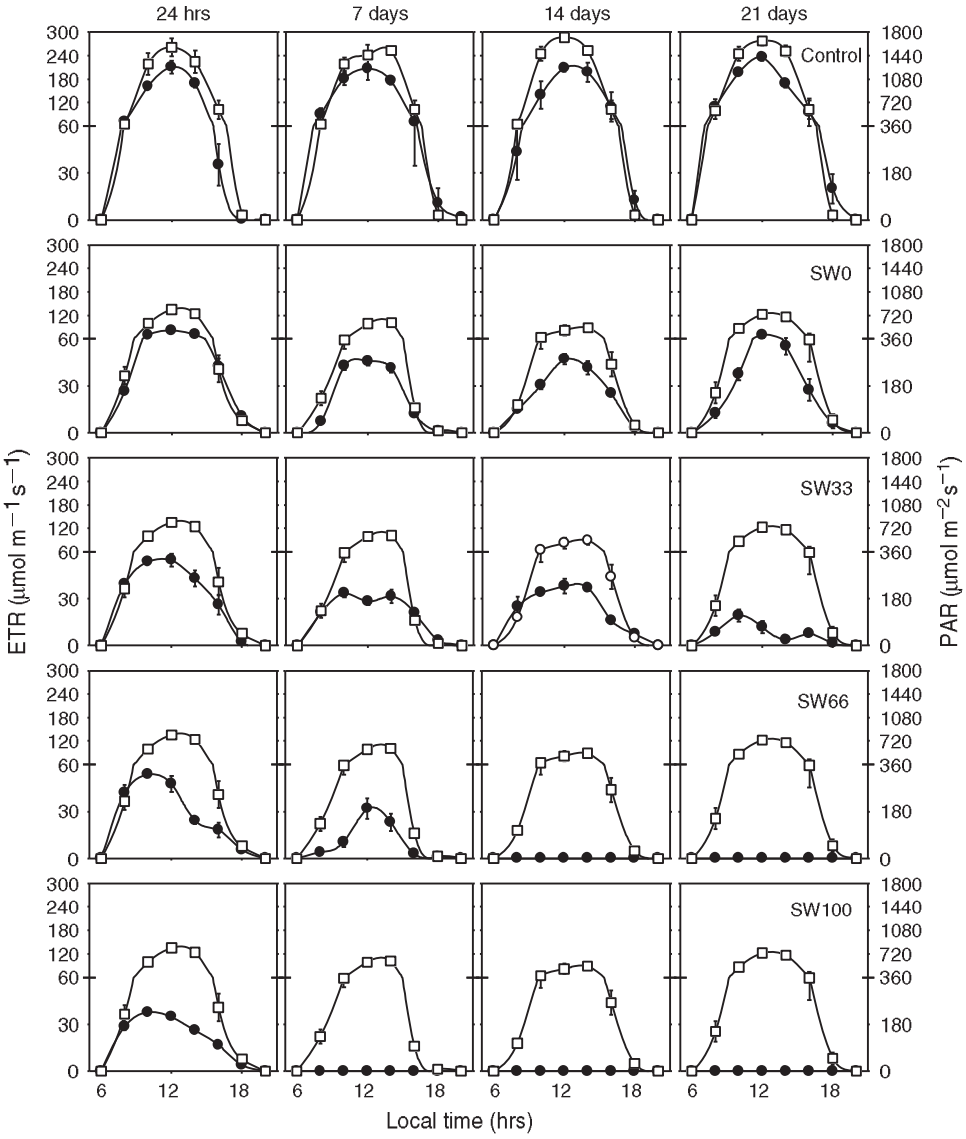


Fig. 2. Underwater response curves of photosynthetic electron transfer rate (ETR; ●) as a function of photosynthetic active radiation (PAR; □) for *A. marina* seedlings in different salinities over a duration of 21 days of submergence (means ± 1 s.d., $n = 15$).

Results

pH drift

In the pH drift experiment (Table 1), the pH of the water decreased continuously in darkness and increased in light. In light, the pH increase was greater in freshwater than in seawater, while in darkness, pH decreased and no significant differences were recorded between the freshwater and seawater treatments. This is a strong indication that a net photosynthetic carbon uptake is continuing underwater when in light, causing a decrease in CO_2, which will result in an increasing pH (Axelsson 1988). Also, it appears that such an uptake was higher in freshwater than in seawater.

ETR during submergence

The photosynthetic response of ETR vs. PAR for seedlings of all three species indicated a progressive decline in photosynthetic rates with increasing underwater duration and increasing salinity. The tolerance to both submergence time and salinity, however, differed between species. Photosynthesis in seedlings of *B. gymnorrhiza* and *A. marina* continued throughout the 21 days of submergence in salinities of up to 33% seawater (Figs 1 and 2). Seedlings of *H. littoralis* maintained photosynthesis for 14 days in freshwater and only seven days in a salinity of 33% seawater (Fig. 3). In the higher salinities, *B. gymnorrhiza* was the most tolerant, maintaining a (reduced) photosynthetic rate for up to 14 days in 66% seawater and for seven days in full seawater. *A. marina* maintained photosynthesis for up to seven days in 66% seawater, but all photosynthetic activity ceased in less than seven days in full seawater. Leaf degeneration and detachment also increased with increasing salinity for all species in a trend similar to that of photosynthesis for each species. Detachment was gradual and followed after the cessation of photosynthesis in each species.

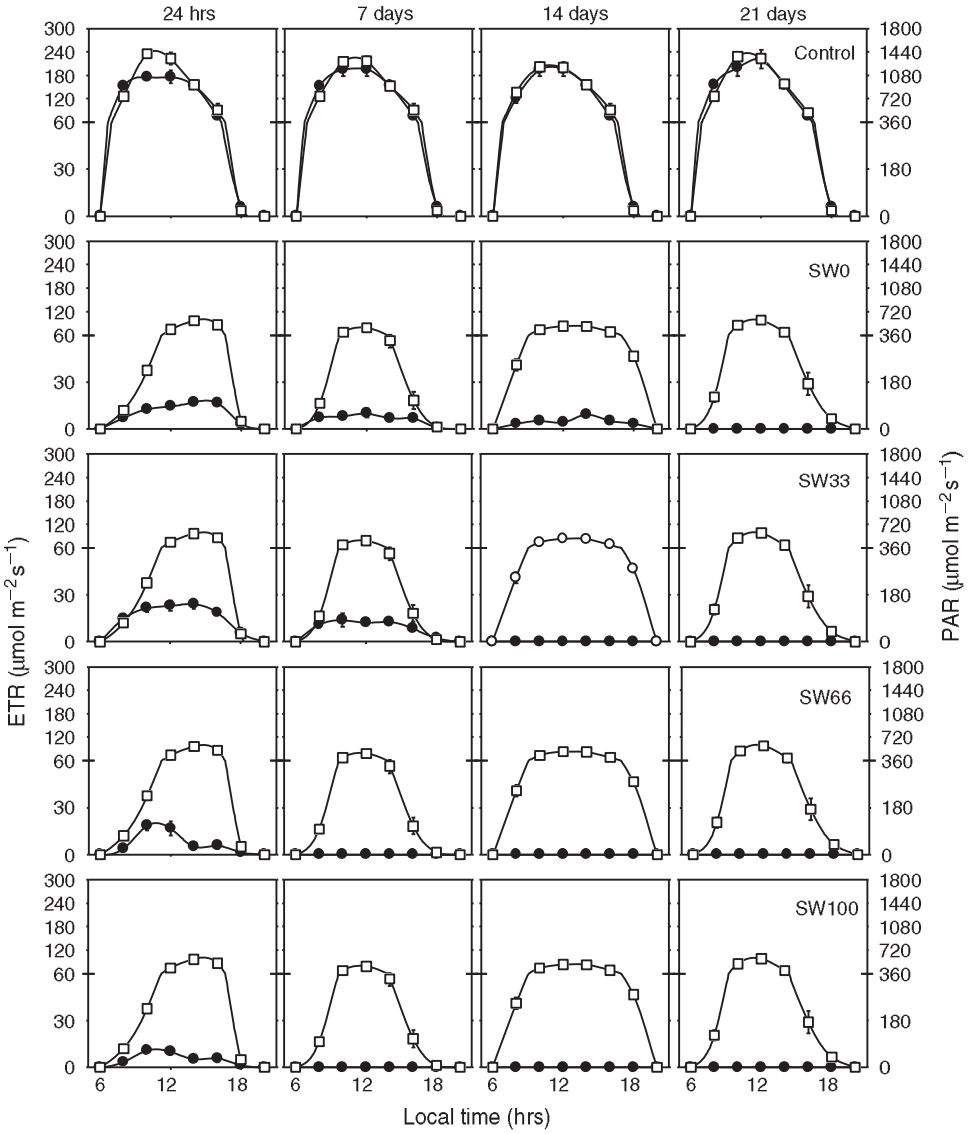


Fig. 3. Underwater response curves of photosynthetic electron transfer rate (ETR; ●) as a function of photosynthetic active radiation (PAR; □) for *H. littoralis* seedlings in different salinities over a duration of 21 days of submergence (means ± 1 s.d., $n = 15$).

The duration of submergence caused significantly declining rates of ETR within species for *B. gymnorrhiza* ($F = 4.750$, $Fcrit = 3.490$, $P = 0.021$) and *H. littoralis* ($F = 9.671$, $Fcrit = 3.490$, $P = 0.002$). Significant effects of both salinity ($F = 5.288$, $Fcrit = 2.816$, $P = 0.003$) and underwater duration ($F = 3.467$, $Fcrit = 2.816$, $P = 0.023$) on rates of ETR were observed between species. Overall, maximum diurnal values of ETR declined in the order of *A. marina* > *B. gymnorrhiza* > *H. littoralis*.

Stress as indicated by maximal photosynthetic yield (Fv/Fm)

Significant differences between species (Table 2) in Fv/Fm were observed within and between salinities over extended underwater durations. Seedlings of *A. marina* displayed higher but more rapidly decreasing values of Fv/Fm in all salinity treatments with greater underwater durations than *B. gymnorrhiza* or *H. littoralis*. *Heritiera littoralis* had the lowest Fv/Fm values (Table 3). For all species, the declining Fv/Fm trend corresponded to that of ETR (Figs 1–3). In the highest salinity treatments in which a particular species maintained photosynthesis for at least 14 days – that is, 100%, 66%, and 33% seawater – the underwater Fv/Fm compared with that of the control plants represented 71%, 85%, and 19% declines for *B. gymnorrhiza*, *A. marina*, and *H. littoralis*, respectively. However, *B. gymnorrhiza* survived longer in the highest tested salinity level.

Survival and recovery

Seedlings were deemed dead when all photosynthetic activity had ceased. By this criterion, *B. gymnorrhiza* survived for a maximum of seven days in 100% seawater, while *A. marina* survived the first seven days of underwater stress only in salinities of up to 66% seawater. For *H. littoralis*, all seedlings

in salinities above 33% seawater died within the first five days. When surviving seedlings of *B. gymnorrhiza* and *A. marina* were kept in the air after termination of the submergence experiment, three of the five seedlings from each treatment (i.e., freshwater and 33% seawater) displayed signs of post-stress recovery, as they sustained green stems and new bud formation. However, these signs of recovery persisted for only three days for *A. marina* and five days for *B. gymnorrhiza*, given normal watering with freshwater twice a day, after which all seedlings died.

Discussion

Terrestrial plants cope with submergence in different ways. Some can maintain carbon fixation during complete submergence through means of specialized carbon acquisition mechanisms, allowing them to acquire carbon from the surrounding seawater (Mommer 2005). In other plants, which lack this ability, photosynthesis stops because of the limited availability of CO_2 and/or light; this will result in loss of biomass, eventually causing plant death (Mommer and Visser 2005). However, even when plants are unable to acquire CO_2 from the water, limited photosynthesis may continue through the recycling of respiratory released CO_2, thereby alleviating the effects of submergence (Mommer and Visser 2005; Voesenek *et al.* 2006). Our results indicated that, even though prolonged submergence had a strong negative effect on all studied mangrove seedlings, some CO_2 uptake was probably continuing (as indicated in pH drift experiment), allowing the more resilient species, e.g. *B. gymnorrhiza,* to survive longer. It is also possible that because inorganic carbon is in less available forms in seawater than in freshwater (due to its higher pH, see e.g. Beer *et al.* 2002), some of the negative effects caused by the higher salinities might be caused by the lower availability of accessible forms of inorganic carbon, causing both a loss in the build-up of energy reserves as well as a possible stress to the photosynthetic apparatus due to oxidative stress (from excess energy captured by the leaf but not spent in carbon fixation).

The markedly reduced Fv/Fm with elevated salinity and prolonged submergence also indicated an injury caused to the photosynthetic apparatus. Such injury was also probably detrimental to the recovery of survived seedlings that were abruptly exposed from submergence to full solar radiation. The significant effect of submergence expressed through the depressed Fv/Fm ratio demonstrates that the ratio can be used as a sensitive indicator of the efficiency of photochemical processes in the photosynthetic apparatus and overall photosynthetic activity of stressed plants (Roháček 2002; Roháček *et al.* 2008). This is relevant because one of the first responses of plants to stressful conditions is a decrease in the rate of photosynthesis (Fracheboud and Leipner 2003). The invention of field-portable, user-friendly and non-destructive, quantitative and diagnostic chlorophyll fluorometers (Maxwell and Johnson 2000; Roháček *et al.* 2008) has supported the use of photosynthetic chlorophyll

Table 2. Summary results of significance values from ANOVAs *F*-test ($P < 0.001$) on pre-dawn Fv/Fm in different salinities (0–100% seawater) and durations (1–21 days) of underwater stress

Species	Source of variation	*F*	*F-crit*	*P*
B. gymnorrhiza	SW0 × 21 days	237.2	3.006	5.07^{-14}
	SW33 × 21 days	641.4	3.055	1.44^{-16}
	SW66 × 14 days	392.5	3.287	1.80^{-14}
	SW100 × 7 days	373.2	3.885	1.57^{-11}
	All Salinities × All Durations	432.9	1.939	1.69^{-43}
A. marina	SW0 × 21 days	65.46	3.179	1.75^{-08}
	SW33 × 21 days	218.1	3.179	9^{-12}
	SW66 × 7 days	235.6	4.256	1.69^{-08}
	SW100 × 14 days	90.31	3.196	1.20^{-10}
	All Salinities × All Durations	143.2	1.944	4.31^{-32}
H. littoralis	SW0 × 14 days	1456.9	3.238	1.04^{-19}
	SW33 × 14 days	2847.0	3.287	6.9^{-21}
	All Salinities × All Durations	1770.7	2.459	8.39^{-33}
All species	All Salinities × All Durations	339.5	1.528	1.5^{-102}

Table 3. Underwater Fv/Fm (means ± 1 s.d., $n = 15$) of species comparison in different salinities over an overall duration of 21 days of submergence provided the seedlings were surviving

Species	Salinity	Duration of submergence			
		24 hrs	7 days	14 days	21 days
B. gymnorrhiza	SW0	0.752 ± 0.004	0.699 ± 0.013	0.574 ± 0.048	0.221 ± 0.035
	SW33	0.750 ± 0.011	0.710 ± 0.024	0.152 ± 0.007	0.147 ± 0.002
	SW66	0.221 ± 0.035	0.144 ± 0.042	0.036 ± 0.020	0.000
	SW100	0.532 ± 0.028	0.209 ± 0.023	0.000	0.000
	Control	0.733 ± 0.038	0.733 ± 0.026	0.735 ± 0.025	0.745 ± 0.019
A. marina	SW0	0.772 ± 0.016	0.705 ± 0.014	0.471 ± 0.053	0.378 ± 0.064
	SW33	0.796 ± 0.012	0.667 ± 0.018	0.637 ± 0.016	0.371 ± 0.031
	SW66	0.693 ± 0.065	0.106 ± 0.016	0.000	0.000
	SW100	0.535 ± 0.007	0.000	0.000	0.000
	Control	0.715 ± 0.035	0.716 ± 0.016	0.716 ± 0.035	0.718 ± 0.048
H. littoralis	SW0	0.462 ± 0.002	0.332 ± 0.017	0.080 ± 0.025	0.000
	SW33	0.692 ± 0.009	0.577 ± 0.013	0.000	0.000
	SW66	0.000	0.000	0.000	0.000
	SW100	0.000	0.000	0.000	0.000
	Control	0.715 ± 0.001	0.716 ± 0.015	0.717 ± 0.020	0.717 ± 0.021

fluorescence as a good and powerful tool for rapid analysis and as indicator of overall plant fitness and activated acclamatory and adaptive mechanisms to cope with environmental stresses (Fracheboud and Leipner 2003; Roháček *et al.* 2008; Rovai *et al.* 2013).

Submergence stress in mangrove habitats is evidently complicated by the constant mixing of fresh and saline waters. Our results demonstrated that the negative effects on photosynthesis increased with increases in salinity, suggesting that mangrove areas experiencing prolonged submergence with flooding dominated by saline water will suffer the most. This might explain the observed failure in natural recovery of degraded mangrove stands in the Rufiji delta in Tanzania (Erftemeijer and Hamerlynck 2005) and Tana river delta in Kenya (Wieczkowski 2009) following the high and prolonged flooding that occurred in 1997–98, which apparently disrupted the salinity regimes of the poorly drained and clogged basin depressions of the flood plains (Erftemeijer and Hamerlynck 2005).

B. gymnorrhiza was able to maintain photosynthetic activity for up to a week, regardless of salinity but photosynthesis declined progressively with prolonged underwater duration across salinities. In contrast, *A. marina* and *H. littoralis* could only maintain a week-long underwater photosynthesis in salinities of up to 66% and 33% seawater, respectively. This restricted performance of underwater photosynthesis may explain the immediate effect of sub-lethal conditions that mangrove seedlings face in the event of unprecedented flooding and consequent submergence with an ultimate degeneration of the succession niche. The ability to continue underwater photosynthesis is an important mechanism for avoiding adverse effects of submergence (Voesenek *et al.* 2006). The differences between species in the response to underwater stress suggested that *B. gymnorrhiza* may have an advantage in areas facing persistent inundations, provided that water remains clear enough to allow light penetration. These results provide information for restoration ecology when choosing species for successful replanting in mangrove areas prone to flooding and tidal highs with elevated salinity. *H. littoralis,* a freshwater-bound species confirms its natural location and distribution higher along the river banks and landward side of the intertidal mangroves. For *A. marina* is considered to be broad range species in terms of salinity tolerance (Patel *et al.* 2010), but may not be suitable in areas that are characteristic of persistent flooding. *B. gymnorrhiza* was shown to be the most resilient species and may therefore serve as a successful species when predicted changes in precipitation and sea-level rise result in flooding and persistent salt intrusion into mangrove habitats (Snedaker 1995).

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