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Assessment of tolerances in *Mitragyna parvifolia* (Roxb.) Korth. and *Syzygium cumini* Keels. seedlings to waterlogging

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Abstract

Waterlogging is one of the critical factors controlling the distribution, regeneration, and survival of vegetation in wetlands. Here, we tested the hypothesis that *Mitragyna parvifolia* (Roxb.) Korth. and *Syzygium cumini* Keels, inhabiting the Keoladeo National Park, a Ramsar wetland (Bharatpur, India), are tolerant to waterlogging. The morphological and photosynthetic variables of four-month-old seedlings subjected to waterlogging, along with the concentrations of macro- and micronutrients, were examined. After 35 days, treatment was halted due to high mortality of *S. cumini* seedlings in contrast to that of *M. parvifolia* seedlings. Significant declines in most of the studied variables were observed in both species when compared with their respective controls. In addition, *M. parvifolia* seedlings developed adventitious roots and lenticels and showed an increased root biomass. Based on the results, we concluded that adaptive traits displayed by *M. parvifolia* seedlings facilitate its tolerance to waterlogging in contrast to *S. cumini* seedlings.

Additional key words: adventitious roots; chlorophyll *a* fluorescence; gas exchange; lenticels.

Introduction

Climate change is anticipated to alter the hydrological cycle, which can consequently change the patterns of precipitation and timing of wet and dry seasons globally (Arnell 1999). The increased frequency in extreme precipitation events increases the risks of flooding in most densely populated and low-lying areas, particularly within the Asian and African continents (Parry *et al.* 2007). These changes in the hydrological cycle occurring because of climate change (Erwin 2009) along with human interference (Bassi *et al.* 2014) have had adverse effects on wetlands worldwide. The success of wetland restoration programs largely depends upon several factors, such as the wetland area, wetland type, degree of damage, hydrology of the catchment, land use of the catchment, and ecological function(s) of interest (Kentula 2000). In addition, each wetland plant has a different water requirement and tolerance, which further depends on the age of the plant (Middleton 2002). Flooding, which results in waterlogging (short or long duration) and full submergence (short or long duration, shallow or deep), creates a selection pressure for many traits of terrestrial wetland plants (Colmer and Voesenek 2009), and such interspecific variation strongly impacts species abundance and distribution in flood-prone areas (Bailey-Serres and Voesenek 2008). Nevertheless, flooding is a common phenomenon in wetland ecosystems, gallery forests, and some regions of high rainfall and poor soil drainage (Pezeshki 1994, Kozlowski 1997).

The effective management of natural areas, forests, and agricultural fields depends on the development of various methods to assess plant variables, such as physiological conditions, plant viability, and the presence of plant stress under various environmental conditions (Goltsev *et al.* 2016). A physiological knowledge of plants is required to understand the habitat requirements of native, endangered, and exotic species; however, this knowledge also underlies the understanding of the fundamental niche of a species, which can help in predicting plant response to climate

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Abbreviations: Chl – chlorophyll; ChlF – chlorophyll fluorescence; E – transpiration rate; F_0 – minimal fluorescence yield of the dark-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; KNP – Keoladeo National Park; LA – leaf area; P_N – net photosynthetic rate; MC – *M. parvifolia* control; MW – *M. parvifolia* waterlogged; SC – *S. cumini* control; SW – *S. cumini* waterlogged; WUE – water-use efficiency (= P_N/E).
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change (van Kleunen 2014). Measures, such as photosynthetic capacity, respiration, or transpiration in plants, which incorporate many physiological systems, might directly reflect the fitness of a plant at an individual level; therefore, conservation physiology can help to monitor threats to biodiversity and to predict response to climate change by determining the physiological tolerance of a plant (Cooke and O´Connor 2010). Leaf or canopy gas exchange along with chlorophyll (Chl) fluorescence (ChlF) provides information on a wide range of key biophysical and biochemical limitations to photosynthesis *in vivo* (Long and Bernacchi 2003). The ChlF measurement may be considered as a powerful tool to assess plant vitality under unfavorable conditions because it is simple, noninvasive, reliable, powerful, inexpensive, and a rapid tool to analyze photosynthetic light-dependent reactions (Dąbrowski *et al.* 2016, Kalaji *et al*. 2016). Hence, these measures are used in various fields, such as agriculture, ecology, and environmental studies, for example, photosynthetic adaptability of rye grass varieties to long-term shade (Dąbrowski *et al.* 2015), photosynthetic acclimation in tor grass (Bąba *et al*. 2016), water and drought stress in barley mutants (Janeczko *et al.* 2016), and gas exchange, delayed Chl in a fluorescent ryegrass under salt stress (Dąbrowski *et al*. 2017).

The deleterious effect of flooding occurs because of the anaerobic conditions created in the soil, which result in an "energy crisis" in the root zone area of plants (Armstrong *et al.* 1994, Colmer and Voesenek 2009). Flooding also alters the physical, chemical, and biological conditions within the soil (Pezeshki 1994, 2001). Flooding or waterlogging results in the saturation of soil pores, thereby reducing soil oxygen, which may affect aerobic respiration (Lambers *et al.* 2008). Moreover, seedlings are found to be more sensitive to waterlogging than older plants (Kozlowski 1984). The effects of flooding on plants include the disruption of the carbon–water balance; decreases in the root system, photosynthetic rate, stomatal conductance, and leaf growth, destruction of Chl, premature leaf senescence, abscission, changes to biomass partitioning, and decreases in mineral and water absorption due to lowered root hydraulic conductivity. However, an increase in ethylene and reactive oxygen species is also observed (Drew 1997, Kozlowski 1997, Pezeshki 2001, Mielke *et al.* 2003, Lambers *et al.* 2008, Ashraf 2012, Verma *et al.* 2012, Insausti and Gorjón 2013). Considered together, these changes alter the morphology, physiology, and anatomy of plants, depending upon the species (Pezeshki 1994, Blom and Voeseneck 1996, Kozlowski 1997).

Keoladeo National Park (KNP), Bharatpur, Rajasthan, India, is a United Nations World Heritage Site, a Ramsar wetland of ecological importance, and a managed wetland. Frequent droughts and water scarcity have distressed the hydrology of the park, thus disturbing its ecology (Brar 1996). Furthermore, approximately a century ago, the wetland was carved out of the floodplain of two seasonal rivers (Ghambir and Banganga) (Chauhan and Gopal 2001); however, at present, the creation of embankments along the rivers and other land uses within the catchment have threatened this wetland (Gopal 2013). *Mitragyna parvifolia* (Roxb.) Korth. of the family Rubiaceae and *Syzygium cumini* Keels. of the family Myrtaceae are two predominant and ecologically important plant species within the park. *M. parvifolia* represents a climax community of swamp/riverbed vegetation (Mathur *et al.* 2010); however, a decline in the population of *M. parvifolia* has been observed in this wetland area (Middleton 2009), and this species is listed as an endangered species of Rajasthan due to its overexploitation and habitat destruction (Panwar and Tarafdar 2006). Although *S. cumini* is a pantropical species, which can colonize ravines, degraded land, and waterlogged areas (Hiwale 2015), it is reported to be susceptible to waterlogging (Nema and Khare 1992).

In order to maintain the wetland, the forest department of Rajasthan, India, has adopted several initiatives, such as the construction of dykes and impoundments in the park to inundate the wetland areas, eradication of invasive species, establishment of forest nurseries, rural appraisal programs to raise awareness of wetlands among people, and encouraging research to protect both the flora and fauna of the park. In our field survey in 2012, we observed a good germination of both species within the park; however, a lower number of saplings were observed for *M. parvifolia* as compared to *S. cumini*. In addition, most of the seedlings observed during the survey were situated within the shade of trees, shrubs, and grasses.

Terrestrial wetland plant species have been observed to withstand flooding conditions by the development of various strategies, even allowing them to thrive under such conditions (Banach *et al.* 2009, Pucciariello *et al.* 2014). Moreover, the degree of flooding tolerance varies among species, which further depends upon flooding and plant conditions, such as time, depth and duration, plant age, and edaphic factors (Kozlowski 1984, Ewing 1996). Hence, in the present study, we hypothesized that *M. parvifolia* and *S. cumini* inhabiting a KNP wetland can tolerate flooding/ waterlogging. Therefore, its seedlings can survive and become established under waterlogged conditions. Moreover, as available literature shows, no attempt has been made to date to study the waterlogging tolerance of *M. parvifolia* and *S. cumini* at the seedling stage.

Materials and methods

Plant material and waterlogging treatment: During May 2014, seeds were collected from *M. parvifolia* and *S. cumini* in KNP (27°7'6"– 27°12'2"N and 77°29'5"–77°33'9"E), then the seeds were grown in the garden of the University of Delhi, India, during July 2014. After germination, seedlings were potted in 5-L pots containing

an autoclaved mixture of sand, organic manure, and garden soil (1:1:4), and then transferred to a growth chamber. Based on field observations, the air temperature and relative humidity were maintained at 30/28°C (day/night) and 80–85%, respectively, with a PPFD of 600 µmol (photon) m^{-2} s^{-1} with a 12/12 h (light/dark) photoperiod. Waterlogging was imposed by immersing the pots containing four-month-old seedlings into a tub filled with water up to 8 cm below the top edge of the pot. The water in the pots was topped up as the water levels dropped, whereas seedlings in the control treatment were watered every third day (650 mL).

Plant growth measurements: Seedling height was measured weekly with a measuring scale, whereas leaf area (LA) was calculated by drawing a leaf outline on a graph paper with a pencil and counting the enclosed squares at the end of the experiment.

Plant biomass: The leaves, stems, and roots of the seedlings were harvested after completion of the experiment (35 d), immediately weighed for fresh mass (FM), and then dried in an oven at 60°C until a constant mass was achieved for the measurement of dry mass (DM), following which biomass was calculated.

Plant nutrient analysis: The dried leaf, stem, and root samples were ground to a fine powder, then 0.50 g of the powdered sample was digested in a nitric acid:perchloric acid (1:5) solution (Allen 1974) prior to analysis. The concentrations of Na^+ and K^+ were determined using a flame photometer (*Systronics, Flame Photometer 128,* India). Carbon and nitrogen were determined using a CHNS analyzer (*Vario, Micro-cube*, *Elementar,* Germany). Extractable phosphorous was determined colorimetrically by the ammonium molybdate method (Grimshaw 1974), whereas trace elements were analyzed by an atomic absorption spectrophotometer (*GBC sense AA, Dual*, USA).

Leaf gas exchange and measurement of Chl *a* fluorescence: All measurements of the leaf gas exchange were conducted weekly on mature and fully expanded leaves throughout the experimental period between 8:00 and 12:30 h. Light-response curves were constructed to determine the light-saturated rates of photosynthesis, following which all measurements were carried out at PPFD of 1,000 µmol(photon) m^{-2} s^{-1} using a 2-cm^2 chamber of *Li-Cor 6400XT* with a red-blue light-emitting diode light source (*Li-Cor*, Lincoln, Nebraska, USA) (Bidalia *et al*. 2016). The net photosynthetic rate (P_N), stomatal conductance to water vapor (g_s), and the rate of transpiration (E) were measured using the standard equations (von Caemmerer and Farquhar 1981), whereas water-use efficiency was expressed by the P_N/E ratio.

Chl *a* fluorescence was measured in the same leaves used for measuring gas exchange by the use of the leaf chamber fluorometer *Li-Cor 6400XT* (*Licor-Cor*, Lincoln, Nebraska, USA). The leaves were dark-adapted for 30 min, then a pulse of far red light (FR) was applied to the leaf samples to achieve full oxidation of the primary quinone electron acceptor Q_A. Minimal fluorescence (F_0) was then measured by applying a measuring light (630 nm) of very low light intensity [<1 µmol(photon) m^{-2} s^{-1}], which does not induce any significant electron transfer from PSII, whereas the maximal (F_m) fluorescence was achieved by administering a saturating flash of light (630 nm wavelength) [>7,000 µmol(photon) m^{-2} s^{-1}], which induced maximum fluorescence by PSII (Maxwell and Johnson 2000, Govindjee 2004, Kalaji *et al*. 2014).

Chl estimation: Total Chl, Chl *a*, and Chl *b* were determined in the same leaves as those used for measuring gas exchange and Chl *a* fluorescence. The leaves were immediately stored in ice, then 0.1 g of the leaves was immersed in 7 mL of dimethyl sulphoxide, incubated at 80°C, and the final volume brought up to 10 mL. Optical densities were then measured at 645 and 663 nm (Hiscox and Israelstam 1979) using a spectrophotometer (*Beckman Coulter DU 730,* USA). The concentrations of Chl *a* and Chl *b* were calculated using the following Arnon (1949) and expressed as [mg g^{-1}]:

$$\text{Chl } a = \frac{12.7 \times A_{663} - 2.69 \times A_{645}}{1000 \times W} \times V \quad (1)$$

$$\text{Chl } b = \frac{22.9 \times A_{645} - 4.68 \times A_{663}}{1000 \times W} \times V \quad (2)$$

where A_{645} is the absorbance at 645, A_{663} is the absorbance at 663, W is the fresh mass of leaves [g], and V is the final volume of the solution [mL].

Statistical analysis: Data were assessed for normality using the *Kolmogorov–Smirnov'*s or *Shapiro–Wilk'*s tests, while an independent *t*-test was used to compare the mean values of the control and the waterlogging treatment of both the species at a 0.05 level of significance (α) using the statistical software package *SPSS version 16* (*IBM SPSS*, NY, USA).

Results

Growth and survival: After 35 d of waterlogging, 90% mortality was observed in *S. cumini* seedlings compared to 0% mortality in *M. parvifolia* seedlings. Yellowing of leaves was observed in both species. However, *M. parvifolia* seedlings developed hypertrophied lenticels at the base of the stem and adventitious roots emerged from the stem base, whereas no such morphological alterations were observed in *S. cumini*. Waterlogging treatment significantly reduced the seedling height by 19.1% in *M. parvifolia* and 11.4% in *S. cumini* compared

with the controls (Table 1, Fig. 1). LA, which was calculated at the end of the experiment, was also reduced significantly by the waterlogging treatment in both species (Table 2).

Biomass: A decrease in biomass was observed in both species when compared with controls. As compared with the control, significant reductions in leaf and stem biomass of *M. parvifolia* seedlings were observed (24.8 and 35.4%, respectively), whereas a significant increment was observed in the root biomass (60.9%) (Tables 1, 2). However, as compared with the control, the leaf biomass of *S. cumini* (25.6%) did not decline significantly, whereas the reductions in the stem and root biomass were significant (74 and 46.3%, respectively) after 35 d of waterlogging (Tables 1, 2).

Mineral nutrients: The waterlogging treatment resulted in significant decreases in all macronutrients, such as concentrations of N, P, K, Mg, Ca, and C in leaves, stems, and roots of both species as compared with the controls (Table 3); however, P and N in the leaves and roots did not differ significantly from that of the control in *M. parvifolia* (Table 3), whereas only N was significantly different as compared with the control in *S. cumini* (Table 3).

As compared with the controls, significant decreases in the concentrations of the micronutrients, such as Na, Co, Cr, Cu, Zn, Fe, and Mn in leaves, stems, and roots of both species were observed (Table 4), with an exception of a few elements, such as Na, Cu, and Zn, which did not differ significantly in the stem, and Cr and Zn in the roots of *M. parvifolia* (Table 4), whereas Cr and Zn in the stem and Cu and Zn in the roots did not differ significantly in *S. cumini* (Table 4).

Table 1. Difference in the seedlings height, leaf area (LA), leaf, stem, and root biomass, chlorophyll (Chl) *a*, Chl *b*, total Chl, net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), water-use efficiency (WUE), and maximal quantum efficiency of PSII (F_v/F_m) in the seedlings after 35 days of waterlogging treatments compared with controls. MC – *Mitragyna parvifolia* control; MW – *M. parvifolia* waterlogged; SC – *Syzygium cumini* control; SW – *S. cumini* waterlogged.

Treatment	Height [%]	Leaf area [%]	Leaf biomass [%]	Stem biomass [%]	Root biomass [%]	Chl *a* [%]	Chl *b* [%]	Total Chl [%]	P_N [%]	g_s [%]	E [%]	WUE [%]	F_v/F_m [%]
MC	100	100	100	100	100	100	100	100	100	100	100	100	100
MW	80.89	52.50	75.21	64.57	160.87	34.99	76.39	53.71	24.32	52.50	54.91	33.98	0.96
SC	100	100	100	100	100	100	100	100	100	100	100	100	100
SW	88.55	69.36	74.39	26.00	53.36	12.87	78.30	39.89	6.09	158.20	106.11	11.81	5.26

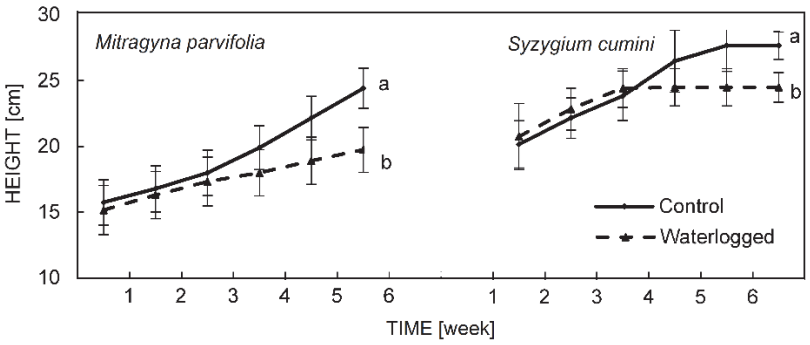

Fig. 1. Seedling height in response to waterlogging, where each value represents mean replicates ± SE (n = 7). Treatments followed by *different letters* are statistically significant ($p \leq 0.05$).

Table 2. Change in the seedling's leaf, stem, and root dry mass, and leaf area after 35 days of waterlogging. Data given are mean ± SE (n = 4). Values followed by *the same letters* are not statistically significant at α=0.05 after *Student*'s *t*-test. MC – *Mitragyna parvifolia* control; MW – *M. parvifolia* waterlogged; SC – *Syzygium cumini* control; SW – *S. cumini* waterlogged.

Parameter	MC	MW	SC	SW
Leaf [g per plant]	11.64 ± 0.25^a	8.76 ± 0.18^b	4.51 ± 0.39a	3.36 ± 0.26^a
Stem [g per plant]	7.68 ± 0.18^a	4.96 ± 0.91^a	3.70 ± 0.13a	0.96 ± 0.02^b
Root [g per plant]	6.30 ± 0.37^a	10.15 ± 0.38^b	2.93 ± 0.23^a	1.56 ± 0.07^b
Leaf area [cm^2 per leaf]	68.75 ± 2.46^a	43.25 ± 2.80^b	35.50 ± 3.32^a	30.00 ± 1.77^b

Table 3. Change in the macronutrients concentration in leaf, stem, and root of the seedlings after 35 days of waterlogging. Data given are mean ± SE (n = 4). Values followed by *different letters* are statistically significant ($p \leq 0.05$) after *Student*'s *t*-test. MC – *Mitragyna parvifolia* control; MW – *M. parvifolia* waterlogged; SC – *Syzygium cumini* control; SW – *S. cumini* waterlogged.

Macronutrients [mg kg^{-1}]	MC	MW	SC	SW
Leaf				
N	27.63 ± 0.06^a	16.52 ± 0.01^b	22.3 ± 0.04^a	11.15± 0.00^b
P	0.46 ± 0.01^a	0.36 ± 0.00^b	0.38 ± 0.02^a	0.36 ± 0.00^b
K	37.51 ± 0.40^a	17.52 ± 0.19^b	7.28 ± 0.37^a	3.25 ± 0.28^b
Mg	1.39 ± 0.01^a	1.17 ± 0.02^b	1.54 ± 0.00^a	1.19 ± 0.00^b
Ca	7.03 ± 0.02^a	0.11 ± 0.00^b	3.39 ± 0.00^a	3.00 ± 0.00^b
Stem				
N	7.64 ± 0.00^a	2.61 ± 0.00^b	12.51 ± 0.01^a	5.67 ± 0.00^b
P	0.39 ± 0.01^a	0.34 ± 0.01^b	0.36 ± 0.00^a	0.33 ± 0.00^b
K	17.73 ± 0.16^a	9.28 ± 0.19^b	7.47 ± 0.18^a	0.75 ± 0.02^b
Mg	1.18 ± 0.00^a	2.88 ± 0.03^b	1.74 ± 0.01^a	1.42 ± 0.00^b
Ca	2.08 ± 0.00^a	5.30 ± 0.00^b	2.32 ± 0.01^a	1.22 ± 0.00^b
Root				
N	11.55 ± 0.01^a	11.21 ± 0.02^b	9.86 ± 0.01^a	12.36 ± 0.00^b
P	0.38 ± 0.02^a	0.35 ± 0.00^b	0.36 ± 0.00^a	0.30 ± 0.00^b
K	15.05 ± 0.07^a	13.31 ± 0.11^b	4.69 ± 0.20^a	2.05 ± 0.03^b
Mg	0.85 ± 0.02^a	1.45 ± 0.02^b	1.10 ± 0.00^a	0.73 ± 0.00^b
Ca	3.25 ± 0.00^a	5.45 ± 0.00^b	4.16 ± 0.00^a	3.06 ± 0.02^b

Table 4. Change in the micronutrients concentration in leaf, stem and root of the seedlings after 35 days of waterlogging. Data given are mean ± SE (n = 4). Values followed by *different letters* are statistically significant ($p \leq 0.05$) after *Student*'s *t*-test. MC – *Mitragyna parvifolia* control; MW – *M. parvifolia* waterlogged; SC – *Syzygium cumini* control; SW – *S. cumini* waterlogged.

Micronutrients [mg kg^{-1}]	MC	MW	SC	SW
Leaf				
Na	7.92 ± 0.14^a	4.54 ± 0.17^b	17.05 ± 0.07^a	10.3 ± 0.31^b
Co	0.13 ± 0.00^a	0.14 ± 0.00^b	0.16 ± 0.00^a	0.07 ± 0.01^b
Cr	0.25 ± 0.00^a	0.24 ± 0.10^b	0.73 ± 0.01^a	0.23 ± 0.06^b
Cu	0.06 ± 0.00^a	0.06 ± 0.00^b	0.03 ± 0.00^a	0.14 ± 0.01^b
Zn	0.01 ± 0.01^a	0.01 ± 0.01^b	0.01 ± 0.00^a	0.02 ± 0.02^b
Fe	1.37 ± 0.01^a	3.48 ± 0.00^b	0.40 ± 0.00^a	0.97 ± 0.00^b
Mn	0.48 ± 0.01^a	0.07 ± 0.00^b	0.05 ± 0.00^a	0.08 ± 0.00^b
Stem				
Na	5.13 ± 0.09^a	7.31 ± 0.13^a	13.05 ± 0.69^a	9.55 ± 0.03^b
Co	0.10 ± 0.00^a	0.14 ± 0.00^b	0.09 ± 0.00^a	0.05 ± 0.01^b
Cr	0.09 ± 0.00^a	0.49 ± 0.03^b	0.23 ± 0.00^a	0.16 ± 0.13^b
Cu	0.04 ± 0.00^a	0.09 ± 0.03^a	0.02 ± 0.00^a	0.10 ± 0.02^b
Zn	0.01 ± 0.01^a	0.01 ± 0.03^a	0.01 ± 0.00^a	0.01 ± 0.012^b
Fe	2.05 ± 0.01^a	1.30 ± 0.03^b	0.36 ± 0.00^a	2.43 ± 0.00^b
Mn	0.07 ± 0.00^a	0.01 ± 0.00^b	0.31 ± 0.00^a	0.08 ± 0.00^b
Root				
Na	4.95 ± 0.11^a	10.42 ± 0.14^b	14.78 ± 0.26^a	9.87 ± 0.35^b
Co	0.15 ± 0.00^a	0.12 ± 0.00^b	0.34 ± 0.18^a	0.09 ± 0.00^b
Cr	0.40 ± 0.00^a	0.30 ± 0.06^a	0.12 ± 0.00^a	0.48 ± 0.051^a
Cu	0.04 ± 0.00^a	0.16 ± 0.02^b	0.02 ± 0.00^a	0.06 ± 0.03^b
Zn	0.02 ± 0.00^a	0.02 ± 0.12^a	0.09 ± 0.00^a	0.01 ± 0.03^a
Fe	1.13 ± 0.00^a	0.45 ± 0.03^b	0.55 ± 0.00^a	0.38 ± 0.00^b
Mn	0.02 ± 0.00^a	0.07 ± 0.00^b	0.62 ± 0.00^a	0.18 ± 0.00^b

Chl concentration: After 35 d of waterlogging, as compared with the controls, significant decreases in the concentrations of total Chl, Chl *a*, and Chl *b* were observed in both species (Fig. 2).

Gas exchange and Chl fluorescence: Waterlogging significantly affected the gas exchange variables (Fig. 3). In *M. parvifolia*, P_N declined by approximately 75%, whereas g_s, *E*, and WUE declined by 47.5, 45.1, and 60%, respectively (Table 1, Fig. 3*A–D*). Similarly, in *S. cumini*, P_N and g_s declined significantly by 93.9 and 58.2%, respectively, whereas *E* and WUE increased by 6 and 60%, respectively (Table 1, Fig. 3*A–D*). The trends of these variables fluctuated in both species. The values of F_v/F_m decreased in both species as compared with the controls; however, the decline was significant only in the case of *S. cumini* after 35 d of waterlogging (Fig. 3*E*).

Discussion

Plant survival and growth: The results from our study suggest that seedlings of *M. parvifolia* were relatively more tolerant to waterlogging than those of *S. cumini*. Seedling survival was 10% in *S. cumini* in contrast to 100% in *M. parvifolia* after 35 d of the experiment. High mortality in *S. cumini* seedlings suggests its failure to combat flood-related injuries resulting from anaerobic conditions in the root systems, which reduces the energy yield of carbohydrates and increases the production of toxic compounds such as ethanol or lactate (Schaffer *et al.* 1992, Joly and Brandle 1995). Yellowing of leaves was observed in both species under waterlogged conditions, which is a common visual symptom under waterlogging (Smethurst *et al.* 2003). However, *M. parvifolia* seedlings displayed the necessary adaptive traits such as (*1*) the formation of adventitious roots which oxidize the rhizosphere, thereby converting soil-borne toxins into less harmful compounds and supporting shoot growth by providing water, minerals, and hormones (Kozlowski 1997) and (*2*) the formation of lenticels that act as a pathway for gas exchange (Kozlowski and Pallardy 2002). The phytohormone auxin is generally responsible for the formation of adventitious roots during flooding (Lambers *et al.* 2008). Various researchers have observed a reduction in height in many species, such as *Platanus occident* (Tang and Kozlowski 1982) and *Pterocarya stenoptera* (Li *et al.* 2010). In contrast, Yamamoto *et al.* (1995) in *Fraxinus mandshurica* and Parolin *et al.* (2001) in an Amazon floodplain tree species found that height was not severely affected by waterlogging. A significant decline in height was observed for both species (Fig. 1), which can be explained by a low oxygen supply to the root system, a decrease in the capacity of plants to absorb water and nutrients, and a decline in synthesizing hormones such as cytokinins (Jackson 1993, Oliveira *et al.* 2010). The reduction in growth also depends on the depth of water above the soil surface (Malik *et al.* 2001). Flooding is reported to suppress leaf formation and expansion, and causes premature leaf senescence and abscission in plants (Kozlowski 1997). A significant reduction in LA was observed in both species (Table 2). However, this decrease can be explained by the reduction in carbon uptake in the seedlings, as reported in *Jatropha curcas* (Verma *et al.* 2012) and *Genipa americana* (Mielke *et al.* 2003).

Plant biomass: Decreases in dry mass as compared with those in controls were observed in many species under the flooding treatment. It has been also reported that fungal infection causes root decay in flood-sensitive species (Stolzy and Sojka 1984). Reductions in biomass were observed in both species, except for the root biomass in *M. parvifolia*, which showed a significant increase (Table 1). Seedlings of *S. cumini* showed root rot and died after 35 d of waterlogging, which can be linked to the significant reduction in root biomass (60.9%) and reflects the disability of *S. cumini* seedlings to adapt to waterlogging. The observed decrease in biomass was related to slow metabolic activity under anoxia, which impairs mitochondrial electron transport, glycolysis, and oxidation of NADP, H^+, and ATP synthesis, and leads to the production of acetaldehyde, ethanol, and lactic acid (Pezeshki 1994, Drew 1997, Gibbs and Greenway 2003, Mielke *et al.* 2005). The increase in root biomass in *M. parvifolia* was partly a result of the formation of adventitious roots, as observed in *Muehlenbeckia florulenta* by Capon *et al.* (2009). Despite lower height,

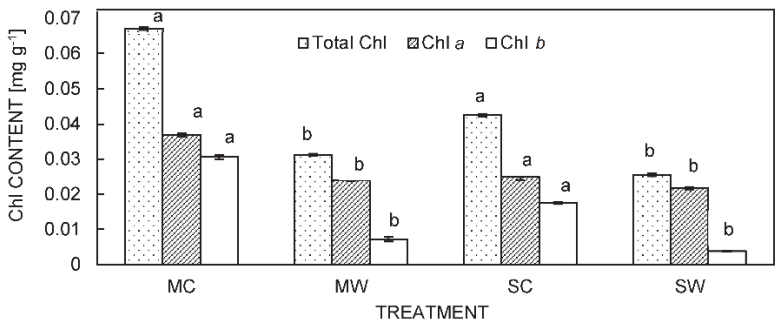

Fig. 2. Leaf chlorophyll (Chl) *a*, *b* and total Chl in response to waterlogging where each value represents mean replicates ± SE ($n = 4$). Treatments followed by *different letters* are statistically significant ($p \leq 0.05$). MC – *Mitragyna parvifolia* control; MW – *M. parvifolia* waterlogged; SC – *Syzygium cumini* control; SW – *S. cumini* waterlogged.

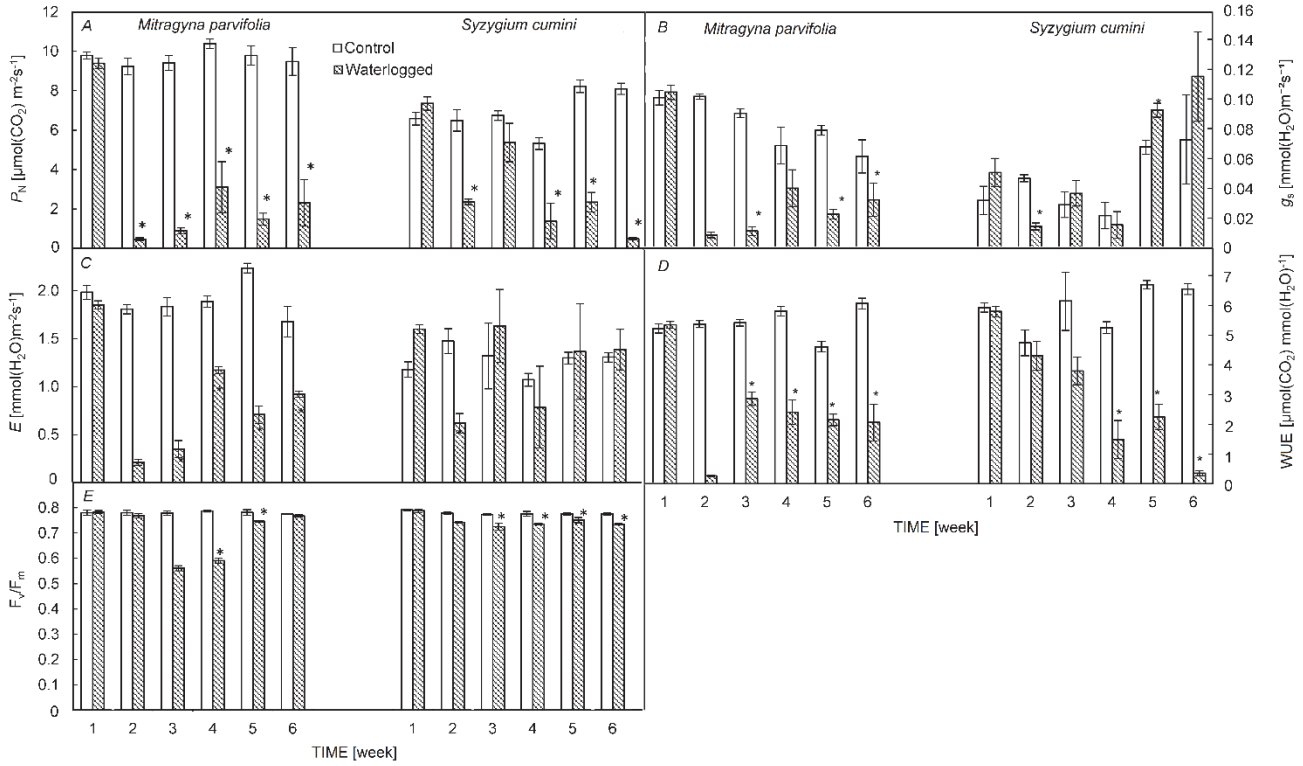

Fig. 3: Effect of waterlogging on the net photosynthetic rate (P_N; *A*), stomatal conductance (g_s; *B*), transpiration rate (*E*; *C*), water-use efficiency (WUE; *D*), and F_v/F_m (*E*) during 35 days. Each value represents the mean ± SE (n = 4). Treatments followed by *different letters* are statistically significant ($p \leq 0.05$).

M. parvifolia showed higher biomass than that of *S. cumini*, reflecting the carbon investment in leaf, stem, and root biomass by the plant rather than an increase in height.

Plant mineral nutrient concentrations: Nutrients play an essential role in plant growth and development (Perkins *et al.* 2011). The concentrations of N, P, and K have been found to be reduced under waterlogging (Kozlowski 1997). Similar results were observed in the current study for both *S. cumini* and *M. parvifolia* seedlings, except for P and N of the leaves and roots (Table 3). Flooding disrupts the mineral composition of plants because soil aeration influences the mineral absorption by the roots (Yang *et al.* 2013). At the same time, the absorption of mineral elements is accomplished through active transport, which is closely related to the generation of ATP from respiration in plant roots (Huang *et al.* 2007). The lowering of nutrient status in plants may trigger the formation of cluster roots on lateral adventitious roots in some plant species, *e.g.*, *Hakea* (Poot and Lambers 2003). The formation of adventitious roots in *M. parvifolia* can be associated with an imbalance in mineral status. A study by Chen *et al.* (2005) on *Lepidium latifolium* found that the concentrations of N, P, K, and Zn decreased, Mn and Fe increased, and P, N, K, and Zn were higher in roots. In contrast, Gimeno *et al.* (2012) observed an increase in leaf Ca, Mg, and P in *Jatropha curcas*. The increase of Na^+ concentration in the roots of *S. cumini* reflects a decrease in the selectivity of K^+/Na^+ uptake by roots in favor of Na^+ and retards the transport of K^+ to the shoots (Thomson *et al.* 1989). Such ion selectivity was also observed in *L. latifolium* (Chen *et al.* 2005).

Chl concentrations under waterlogging: Leaf chlorosis is commonly observed in plants under stress, and is a condition that leads to senescence and is associated with a concomitant decline in the concentration of photosynthetic pigments (Webb and Fletcher 1996). A reduction in Chl contents in leaves is common under flooding/waterlogged conditions (Webb and Fletcher 1996, Yordanova and Popova 2001). In our experiment, the contents of total Chl, Chl *a*, and Chl *b* significantly decreased in both species under waterlogged conditions (Fig. 2), thereby confirming the results of previous studies in other plants, such as *Arachis hypogaea* (Bishnoi and Krishnamoorthy 1992), *Ricinus communis* (Gadallah 1995), white and red clover (Simova-Stoilova *et al.* 2012), and *Pyrus persica* (Insausti and Gorjón 2013). Such a decrease is considered as a protection mechanism employed within photosynthetic structures, which reduces sunlight absorption and avoids photo-oxidation, as explained by Du *et al.* (2012) in *Populus simonii* and *P. lux*. Chl *b* is reported to be more sensitive to flooding than Chl *a* (Ashraf and Arfan 2005),

and we observed a larger decrease in Chl *b* than that in Chl *a*. However, since Chl *b* is an accessory pigment of the LHC, its decline can result in reduced photochemical efficiency as well as photoinhibition. However, under waterlogging, a decline in Chl *b* may have a significant effect on LHCII complexes containing Chl *b* in the mature thylakoid membranes (Green 1988, Sairam *et al.* 2009).

Leaf gas exchange and Chl *a* fluorescence under waterlogging: Reductions in gas exchange in both species confirmed the results of previous studies of many flood-tolerant and flood-intolerant species. Stomatal limitations are considered to be the initial cause of a decrease in photo-synthesis during flooding (Pezeshki 1993, Kozlowski 1997). However, during a longer period of flooding, non-stomatal limitations occur, such as pigment degradation and alteration of enzymes in the Calvin Cycle, which lead to a decline in carboxylation efficiency (Pezeshki 2001). In addition, feedback inhibition by starch accumulation in leaves due to lack of transport by roots was observed in watermelon (Yetisir *et al.* 2006). The significant decline in P_N and g_s observed in *M. parvifolia* (Fig. 3) can be explained by stomatal closure due to hypoxia, which limits P_N. Similar results were obtained in *Momordica charantia* (Liao and Lin 1994) and certain herbaceous species (Jackson and Drew 1984). The recovery of P_N is related to the formation of adventitious roots and lenticels, which are further linked to the reopening of stomata that had closed shortly after the flooding was initiated (Gomes and Kozlowski 1980). However, *S. cumini* seedlings showed high fluctuations in gas exchange while still alive (Fig. 3). The stomatal closure may be related to a decrease in root hydraulic conductivity (Andersen *et al.* 1984, Davies and Flore 1986), which is a common response observed in both tolerant and intolerant woody plants under flooding (Kozlowski 1997, Bertolde *et al.* 2010). Newsome *et al.* (1982) observed that flooding did not induce stomatal closure in *Ulmus americana* seedlings. Liu and Dickman (1992) observed stomatal closing after 9 d in hybrid *Populus* clones. *Quercus macrocarpa* seedlings failed to reopen stomata (Tang and Kozlowski 1982), whereas Harrington (1987) observed no stomatal closing in *P. trichocarpa*. In our study, the *E* was correlated with g_s in both species (Fig. 3*B,C*). This trend is also commonly observed in other species such as *Melaleuca alternifolia* (Jing *et al.* 2009). Greater WUE is commonly observed in plants under flooding conditions (Bertolde 2012). In our study, we did not identify any increase in WUE in both species, which supports the results of Mielke *et al.* (2003) in their study on *Genipa americana*, the results of Arbona *et al.* (2009) in citrus, and those of Islam (2004) in tamarack; however, our results were not supported by the findings of Islam (2004) in a study on black spruce.

The leaf Chl *a* fluorescence or the ratio of F_v/F_m is considered to be an important indicator of the effects of environmental stresses and the status of PSII machinery (Maxwell and Johnson 2000, Kalaji *et al.* 2016). This is a widely used technique because of its rapid and noninvasive nature, and provides detailed information on the state of PSII (Papageorgiou and Govindjee 2011, Murchie and Lawson 2013). A decrease in the value of F_v/F_m is a good indicator of photoinhibitory impairment resulting from waterlogging stress (Mielke *et al.* 2003, Bertolde *et al.* 2010). In our experiment, the values of F_v/F_m declined significantly in *S. cumini* seedlings, possibly reflecting photodamage in *S. cumini*, as observed in *Myrica cerifera* (Naumann *et al.* 2008) under flooding. The values of F_v/F_m of *M. parvifolia* seedlings showed no significant decrease during the experimental period, except at 21 and 28 d, then it recovered (Fig. 3*D*). However, F_v/F_m values were within the range for healthy plants (Percival *et al.* 2003). Similar results were obtained by Meilke *et al.* (2003) in *Genipa americana*, which indicated no photodamage.

Conclusion: Based on our results, we rejected our hypothesis that both *M. parvifolia* and *S. cumini* are adapted to waterlogging because they inhabit a wetland. *S. cumini* seedlings were highly susceptible to water-logging because this species lacks adaptive traits required to survive under flooding conditions, ultimately leading to impairment of gas exchange, nutrient imbalance, de-creased growth, chlorophyll loss with yellowing of the leaves. In contrast, *M. parvifolia* seedlings survived water-logged conditions. In addition, Chl *b* was more sensitive to waterlogging than Chl *a* in both species. However, the performance of *M. parvifolia* seedlings also declined under waterlogging, although gas exchange recovered after the development of adventitious roots and lenticels. The tolerance of *M. parvifolia* to flooding may increase survival of its seedlings in comparison to *S. cumini* seedlings in waterlogged areas in the KNP. Prolonged water scarcity in the KNP allowed other species to establish themselves in the forest along with established species. The survival and establishment of the species depends on the prevailing biotic and abiotic environmental conditions at the particular time. The presented results can be considered as a baseline study for designing field-based experiments. The results of the present study provided insight into waterlogging tolerance in both species; however, results are difficult to predict under field conditions because other factors, such as plant age, depth, and duration of flooding, soil conditions, and the presence of monsoon also determine seedling survival. However, understanding the physical tolerances of *M. parvifolia* and *S. cumini* can assist land managers and policy planners in the formulation of strategies for restoration, plantation, and protection of the species across regions with similar environmental conditions. Furthermore, flood tolerance is an important trait for species survival in a wetland; however, rapid changes in environmental conditions can alter the future composition of vegetation within an ecosystem.

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