Responses to Flooding of Two Riparian Tree Species in the Lowland Tropical Forests of Thailand

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ABSTRACT

Responses of riparian woody species, especially in the tropical forests of Thailand, under flooding condition remain unknown. The effects of flooding on growth of the native species, *Hydnocarpus anthelminthicus* and *Xanthophyllum lanceatum*, which dominate in the lowland tropical forests in the East of Thailand, were observed during 16 weeks. The growth and morphological responses were determined in one-year-old seedlings, which stems were submerged at a level of 3 cm above the soil surface (flooded). They were compared to the control (unflooded) at every 2, 4, 8, 12, and 16 weeks. Flooding did not suppress shoot elongation in *H. anthelminthicus* and *X. lanceatum* over the study period. In general, leaf, stem, and root biomass were not significantly different between flooded and unflooded seedlings in both species. Adventitious roots were found in flooding seedlings of both species, while hypertrophied lenticels were not formed during the submergences. In addition, senescence, necrosis, abscission, or mortality were not observed in the flooded seedlings in this study. Preliminarily, *H. anthelminthicus* and *X. lanceatum* could be considered as potential species for restoring the riparian forest, especially in the studied region.

1. INTRODUCTION

Flooding negatively affects growth and development of many woody plants (Kozlowski, 1997). Numerous reports have demonstrated the effects of flooding on morphological and physiological responses in both gymnosperms and angiosperms (Yamamoto and Kozlowski, 1986; Yamamoto, 1992; Lopez and Kursar, 1999; Sakio, 2005; Higa et al., 2012). Vegetative and reproductive growth suppression, alternation of plant anatomy, and promotion of senescence and mortality usually occur in most terrestrial plants under flooding condition. Plants that tolerate waterlogged conditions can survive by using the complexity of interactions of morphological, anatomical, and physiological adaptations, such as formation of hypertrophic stem growth, aerenchyma tissue and adventitious roots (Kozlowski and Pallardy, 1979; Yamamoto et al., 1995; Wang and Cao, 2012; Oliveira et al., 2015). Such various reactions to tolerate flooding depend on plant species and genotype, age, properties of the floodwater, and time or duration of flooding (Kozlowski, 1984).

Riparian forests occur along bodies of water, such as streams, lakes, and rivers, and they play an important role by providing environmental services to both aquatic and terrestrial ecosystems (Broadmeadow and Nisbet, 2004; Gunderson et al., 2010). Particularly, riparian vegetation is crucial for freshwater landscape by regulating flow of sediment and nutrients (Luke et al., 2007; Mayer et al., 2007), moderating light and temperature for aquatic life (Broadmeadow and Nisbet, 2004), filtering the heavy metals from agricultural land (Zhang et al., 2010; Pavlovic et al., 2016), providing habitat for forest species (Waiboonya et al., 2016; Moungsrimuangdee et al., 2017a) and reducing soil erosion and stabilizing the stream banks (USDA National Agroforestry Center, 1997).

Phra Prong River, the origin of Bang Pakong River, is one of the most important rivers in the East of Thailand. It represents a freshwater ecosystem for

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biodiversity conservation and supplying foods and water use for the local people livelihood (Moungsrimuangdee et al., 2017b; Yodsanga et al., 2017). Riparian forests along Phra Prong River have dramatically declined in the last decades due to an expansion of agricultural land and irrigation management practices. Consequently, the distribution and regeneration of native tree species have been severely affected (Moungsrimuangdee et al., 2015).

Regular and irregular flooding are considered to be major factors influencing riparian species diversity and habitat (Uowolo et al., 2005). Few studies have focused on the effects of flooding on riparian species composition and abundance, especially in the tropical forests of Thailand. In addition, the flood-tolerant trees of the tropical forests in this region have also rarely been investigated. Therefore, in this study, we focused on the responses of *Hydnocarpus anthelminthicus* and *Xanthophyllum lanceatum*, the native and dominant tree species of Phra Prong riparian forest of the Eastern Thailand, to flooded condition. Currently, constitutive defense responses to cope with the stress of these species are still not known. Flooded responses of the native species could explain the habitat and ecological characteristics of these species and provide more insight into riparian restoration efforts which are highly required in this area.

2. METHODOLOGY

2.1 Study site and study species

Hydnocarpus anthelminthicus Pierre ex Laness. (Achariaceae) and *Xanthophyllum lanceatum* J. J. Sm. (Polygalaceae) were selected in this study. They are commonly found, and classified as dominant trees in the riparian forests of Phra Prong River according to our previous studies (Moungsrimuangdee et al., 2015; Nawajongpan and Moungsrimuangdee, 2016; Moungsrimuangdee et al., 2017a). In addition, both species often grow in the freshwater swamp forest of Thailand (Santisuk, 2012). On July 2015, seeds of these species were collected from the mature trees growing naturally in the riparian forest found along the Phra Prong River, located in Watthana Nakhon District, Sa Kaeo Province. Seeds were sown in plastic trays containing sandy soils. Seedlings with at least two pairs of true leaves were transplanted into plastic bags containing a forest soil collected form the riparian forest of Phra Prong River. The plants were raised at the nursery of the Bodhivijjalaya College, Srinakharinwirot University, Sa Kaeo, located close to the river. One-year-old seedlings were transplanted into plastic pots (15 cm × 15 cm × 18 cm), containing the forest soils mentioned above. They were left to grow in the nursery under the same conditions with watering, pesticides and fertilizations for three months. Climatic data (2006-2015) at the study site showed 28.5 ^{o}C mean annual air temperature with 73% mean annual relative air humidity and 1,200 mm annual sum of precipitation (Meteorological Department, 2016).

2.2 Experimental design

On November 2016, seedlings of each species were selected for uniform size and development. The selected seedlings were divided into two treatments, unflooded and flooded, with three replications (35 seedlings per replication). For each treatment, another five seedlings of each species were randomly harvested for biomass analysis at the beginning of the experiment. The average height and stem diameter at ground level of each species at the initial stage were measured. The size of seedlings at the starting time did not differ significantly between the unflooded and flooded seedlings ($p<0.05$, t-test) as shown in Table 1.

Table 1. Size of the seedlings at the initial stage. Data are given as mean±standard error. D0 means stem diameter at ground level.

Species	Unflooded		Flooded	
	Height (cm)	D0 (mm)	Height (cm)	D0 (mm)
Hydnocarpus anthelminthicus	42.37±1.05	4.85±0.12	42.31±1.01	4.43±0.12
Xanthophyllum lanceatum	35.36±0.77	5.52±0.16	35.58±0.84	4.83±0.17

The treatments with flooding were applied by placing the seedling pots in the water-filled containers providing water received from the Phra Prong River at a level of 3 cm above the soil surface (roots and the basal part of the stems flooded). Water was added periodically to keep the water level steadily without changing the water throughout the experiment. The unflooded seedlings were daily watering to prevent soil desiccation. All seedlings were grown in the nursery under the shading net giving 40% of full sunlight.

2.3 Data collection and analysis

Shoot elongation or shoot height, number of leaves, leaf area, biomass, and total nitrogen in leaves were determined after 2, 4, 8, 12, and 16 weeks. Seedling mortality, adventitious roots, hypertrophied lenticels, and leaf chlorosis or necrosis were also observed until the end of the study period. Seven seedlings in each replication of all treatments were harvested at each data collection. All fresh leaves of the harvested seedlings were scanned into JPEG image format using a scanner (Canon Scan MF4800; Canon Inc., Tokyo, Japan). Then leaf area was calculated by using free online software (ImageJ) (https://imagej.nih.gov/ij/index.html) (Moungsrimuangdee et al., 2011). For biomass analysis, all harvested seedlings were separated into leaves, stems and roots. All portions were then separately dried at 70 °C, 48-72 h until samples reached a constant dry weight (University of Idaho, 2009). Composite samples of leaves from each individual replication within the treatment were taken from the dry material for a total nitrogen analysis according to the Kjeldahl method (1883). The differences in the mean values between the treatments were analyzed by using a t-test ($p<0.05$). Statistical analyses were performed with PAST version 3.22 (Hammer et al., 2001).

3. RESULTS

3.1 Shoot elongation

Flooding did not reduce the shoot elongation of *H. anthelminthicus* and *X. lanceatum* throughout the experiment. Besides, the shoot growth of the flooded plants was higher than those unflooded seedlings in all submerged periods (Figure 1 and 2). In *X. lanceatum*, shoots of flooded seedlings distinctly increased in comparison with unflooded seedlings after 12 weeks of the experiment (Figure 2). However, there were no significant differences among the treatments in both species (Figure 1 and 2).

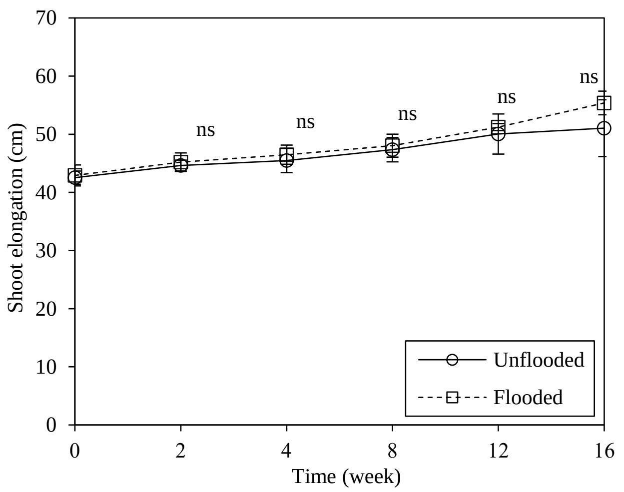

Figure 1. Shoot elongation in flooded and unflooded seedlings of *H. anthelminthicus*. Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at $p<0.05$ by t-test).

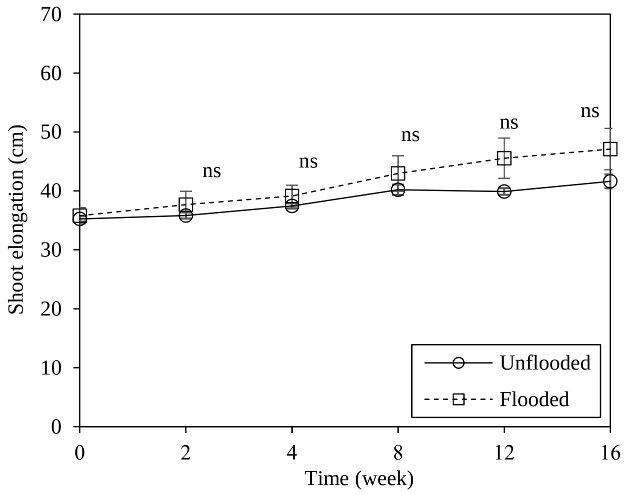

Figure 2. Shoot elongation in flooded and unflooded seedlings of *X. lanceatum*. Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at $p<0.05$ by t-test).

3.2 Number of leaves and leaf area

Leaves slightly decreased in flooded seedlings of *H. anthelminthicus* after 2 weeks of the submergence and gradually increased after 4 weeks until the end of the experiment (Figure 3). The number of leaves was lower in flooded than in unflooded seedlings in all time periods (Figure 3). In *X. lanceatum*, flooded seedlings had almost the same number of leaves as unflooded seedlings in all time periods, except in weeks 8 and 16 in which the flooded were lower than in unflooded (Figure 4). However, *H. anthelminthicus* and *X. lanceatum* leaf numbers did not significantly differ between treatments and periods. Pattern of leaf area was similar in the flooded and unflooded *H. anthelminthicus*. Leaf area decreased after 2 weeks, then slightly increased after 4 weeks of the experiment in both treatments (Figure 5). Flooded *X. lanceatum* reached the highest leaf area after 12 weeks (Figure 6).

3.3 Biomass

Leaf, stem, and root biomass of *H. anthelminthicus* seedlings were not significantly different among the flooded and unflooded treatments within studied periods (Table 2). In general, flooded seedlings of *H. anthelminthicus* showed higher dry weight of leaves, stems, and roots than unflooded, except seedlings after 12 weeks and 16 weeks (Table 2). A similar trend was found in *X. lanceatum*, in which dry weight did not differ significantly among treatments, except in week 4 and week 12, where flooded plants' stem biomass were significantly higher than unflooded (t-test, $p<0.05$, Table 3).

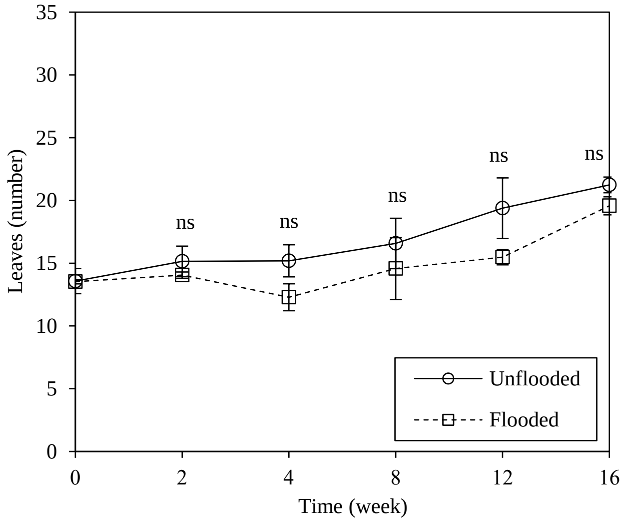

Figure 3. Number of leaves in flooded and unflooded seedlings of *H. anthelminthicus*. Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.05 by t-test).

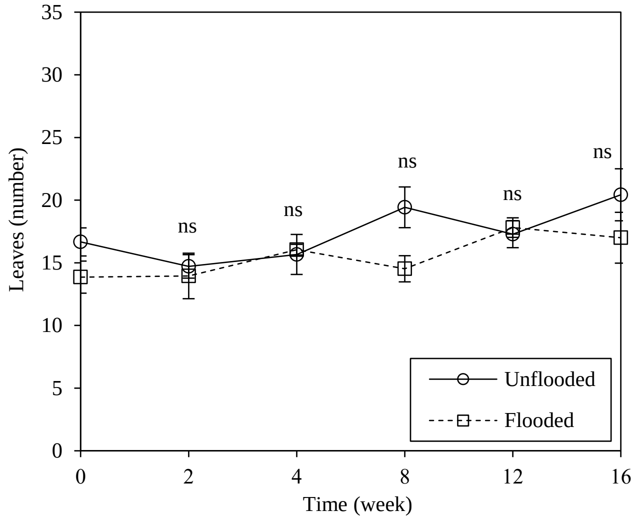

Figure 4. Number of leaves in flooded and unflooded seedlings of *X. lanceatum*. Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.05 by t-test).

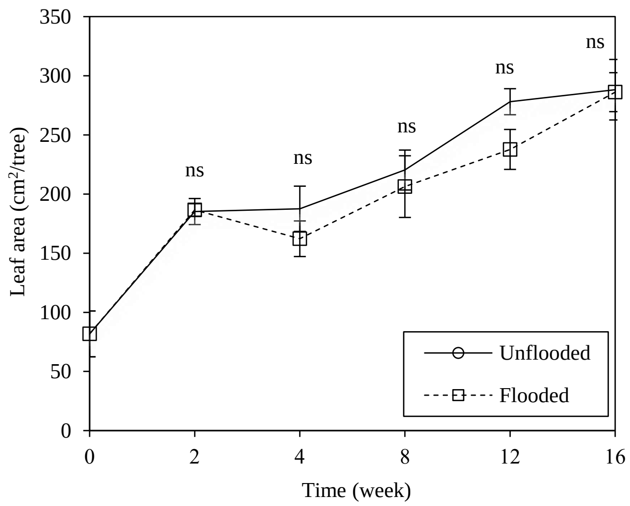

Figure 5. Leaf area in flooded and unflooded seedlings of *H. anthelminthicus*. Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.05 by t-test).

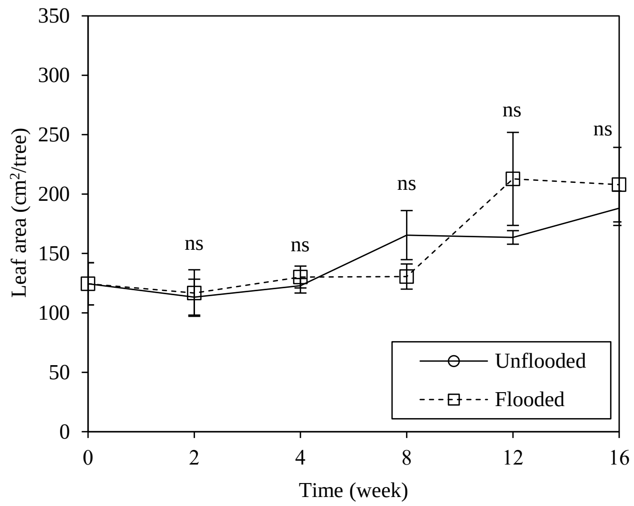

Figure 6. Leaf area in flooded and unflooded seedlings of *X. lanceatum*. Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.05 by t-test).

Table 2. Leaf, stem, and root biomass of *H. anthelminthicus*. Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.05 by t-test).

Biomass	Submerged period (week)					
	0	2	4	8	12	16
Leaves (g)						
Unflooded	1.20±0.25^{ns}	3.67±0.09^{ns}	4.36±0.23^{ns}	3.68±0.42^{ns}	5.36±0.40^{ns}	4.04±0.28^{ns}
Flooded	0.69±0.09	3.89±0.08	4.44±0.19	3.92±0.62	5.50±0.31	3.96±0.16
Stems (g)						
Unflooded	1.66±0.58^{ns}	3.49±0.19^{ns}	4.19±0.44^{ns}	4.89±0.51^{ns}	5.77±0.27^{ns}	4.97±1.06^{ns}
Flooded	0.95±0.24	3.94±0.06	4.44±0.17	5.20±0.58	5.84±0.07	6.00±0.48
Roots (g)						
Unflooded	1.44±0.44^{ns}	4.66±0.15^{ns}	5.53±1.09^{ns}	4.35±0.67^{ns}	5.73±0.35^{ns}	6.13±0.74^{ns}
Flooded	0.73±0.18	4.82±0.24	5.95±0.24	4.37±0.52	5.12±0.18	5.20±0.56
Total (g)						
Unflooded	4.30±1.17^{ns}	11.82±0.13^{ns}	14.08±1.69^{ns}	12.92±1.41^{ns}	16.86±0.53^{ns}	15.14±1.40^{ns}
Flooded	2.37±0.47	12.64±0.34	14.82±0.30	13.49±1.65	16.46±0.22	15.16±1.17

Table 3. Leaf, stem, and root biomass of *X. lanceatum*. Data are given as mean±standard error (* represents the significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.05 by t-test, ns represents the non-significant difference).

Biomass	Submerged period (week)					
	0	2	4	8	12	16
Leaves (g)						
Unflooded	1.47±0.38^{ns}	2.96±0.08^{ns}	3.76±0.12^{ns}	3.32±0.13^{ns}	4.37±0.34^{ns}	3.36±0.32^{ns}
Flooded	1.31±0.32	3.09±0.14	4.93±0.42	2.90±0.31	6.18±0.64	3.62±0.25
Stems (g)						
Unflooded	2.42±0.49^{ns}	3.94±0.31^{ns}	2.95±0.07*	4.14±0.08^{ns}	4.83±0.06*	4.11±0.21^{ns}
Flooded	2.47±0.50	4.27±0.43	3.82±0.20	3.93±0.21	6.16±0.46	4.98±0.62
Roots (g)						
Unflooded	2.16±0.55^{ns}	2.59±0.29^{ns}	4.11±0.47^{ns}	4.49±0.45^{ns}	5.04±0.16^{ns}	5.68±0.28^{ns}
Flooded	2.08±0.39	3.02±0.33	4.57±0.86	3.68±0.18	5.41±0.36	4.55±0.41
Total (g)						
Unflooded	6.05±1.21^{ns}	9.49±0.65^{ns}	10.82±0.45^{ns}	11.96±0.59^{ns}	14.25±0.48^{ns}	13.15±0.45^{ns}
Flooded	5.88±0.74	10.39±0.88	13.32±1.31	10.51±0.30	17.75±1.27	13.16±1.04

3.4 Root:shoot ratio

Changes of root:shoot ratio were analyzed to better understanding the effect of flooding on biomass allocation of the submerged seedlings. The root:shoot ratio of the flooded plants was less than in the unflooded in the *H. anthelminthicus* seedlings, without statistically significant differences over the studied periods (Figure 7). In contrast, flooding was found to significantly reduced root:shoot ratio of *X. lanceatum* at week 12 (t-test, p<0.01) and week 16 (t-test, p<0.05), compared to the unflooded seedlings (Figure 8).

3.5 Total nitrogen

The total nitrogen of *H. anthelminthicus* was significantly less in flooded than in unflooded seedlings at week 2, 4, and 8, but it was slightly increased, almost at the same rate as unflooded, as shown in week 12 and 16 (Figure 9). The differences of total nitrogen among treatments were not found significant in *X. lanceatum* (Figure 10).

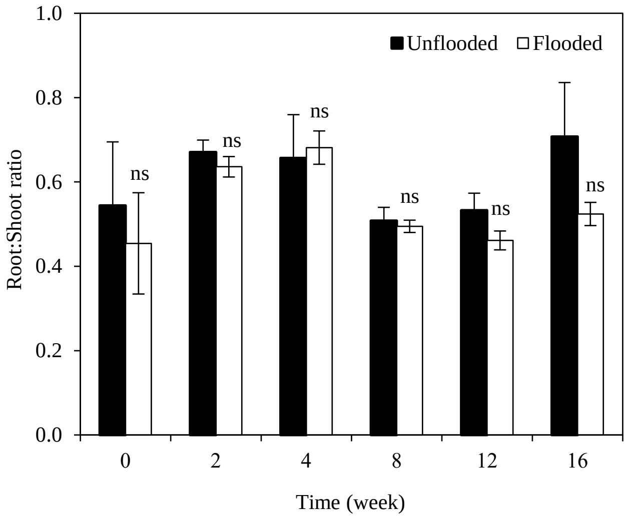

Figure 7. Root:shoot ratio in flooded and unflooded seedlings of *H. anthelminthicus*. Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.05 by t-test).

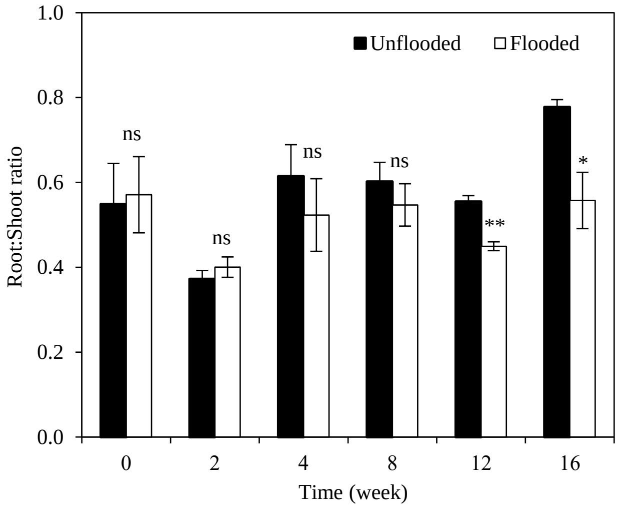

Figure 8. Root:shoot ratio in flooded and unflooded seedlings of *X. lanceatum*. Data are given as mean±standard error (** and * represent the significant difference between the flooded and unflooded seedlings within the same submerged period at p<0.01 and 0.05 by t-test, respectively, ns represents the non-significant difference).

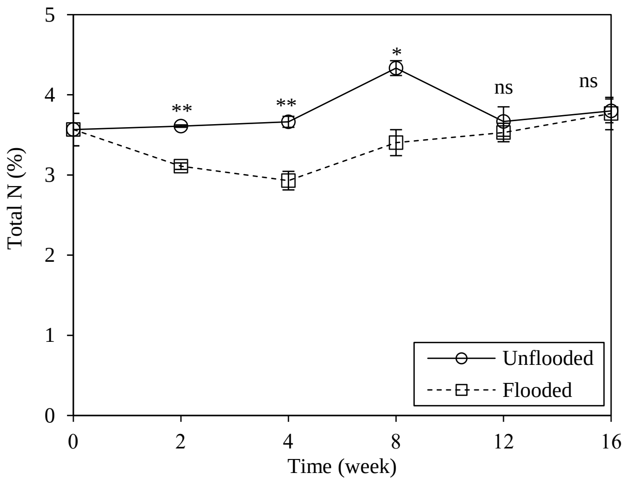

Figure 9. Total N in flooded and unflooded seedlings of *H. anthelminthicus*. Data are given as mean±standard error (** and * represent the significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.01 and 0.05 by t-test, respectively, ns represents the non-significant difference).

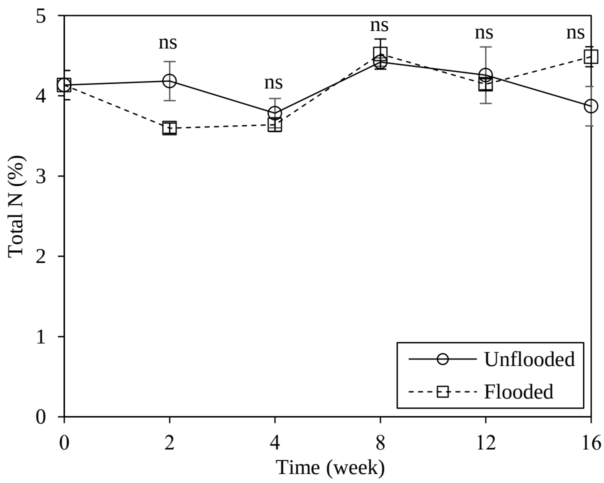

Figure 10. Total N in flooded and unflooded seedlings of *X. lanceatum.* Data are given as mean±standard error (ns represents the non-significant difference between the unflooded and flooded seedlings within the same submerged period at p<0.05 by t-test).

3.6 Adventitious roots

No adventitious roots were found in the unflooded seedlings of both species. The formation of adventitious roots, which were found only in flooded treatments, developed faster in *H. anthelminthicus* than in *X. lanceatum* seedlings. Adventitious roots were formed at week 4 in *H. anthelminthicus*, while adventitious roots of *X. lanceatum* developed later, in week 16 (Figure 11). In addition, the hypertrophied lenticels, an enlarged pore through which gases are exchanged between plant and air, were looked for during the study. These types of lenticels were not found in any of the species.

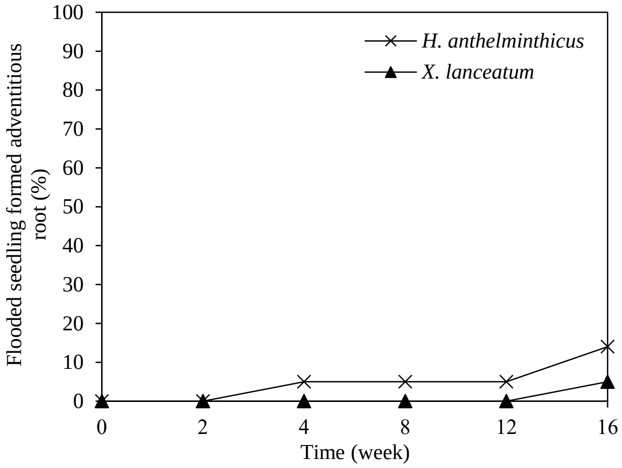

Figure 11. Percentage of flooded seedlings that formed adventitious roots.

4. DISCUSSION

Flooding has been shown to have various effects on riparian species. Shoot growth was found to be inhibited during flooding in several species, such as *Taxodium distichum* (Yamamoto, 1992), *Lepidium latifolium* (Chen et al., 2002), *Alnus japonica* (Iwanaga and Yamamoto, 2008), *Populus euphratica* (Yu et al., 2015) , *Pinus elliottii* (Yang and Li, 2016), and *Alternanthera philoxeroides* (Luo et al., 2018). In contrast, flooding promoted shoot growth and biomass of some riparian species such as *Nyssa aquatica* (McKevlin et al., 1995), *Pterocarya stenoptera* (Yang and Li, 2016), and *Fraxinus excelsior* and *Quercus robur* (Heklau et al., 2019). Plants have responded by adjusting the combination of morphology, physiology, and biochemistry for surviving under the flooding condition such as the recovery of photosynthetic rate and stomatal conductance, enhancement of ethylene production, induction of hypertrophy of lenticels, and formation of adventitious roots containing aerenchyma tissue. In this study, leaf senescence, necrosis, abscission, and mortality were not observed in *H. anthelminthicus* and *X. lanceatum* under the flooding condition. These signs typically occur when plants are under flooding stress. The studied species, therefore, are flood-tolerant species.

Flooding did not affect shoot growth in the two species during 16 weeks of submergence. *X. lanceatum* exhibited a high tolerance to soil flooding by stimulating stem growth and the same rate of leaf growth (number of leaves and leaf area) as the control. *H. anthelminthicus* showed a reduction of leaf growth at week 4, but it gradually increased to an equal number as the control at the end of the experiment. Root growth of flooded *H. anthelminthicus* and *X. lanceatum* was lower than stem growth. This symptom was expressed in the decrease of root:shoot ratio. In woody species, the root typically grows slower than the shoot because the flooding leads to the decay of the root system (Kozlowski, 1997).

Flooding also induces certain morphological changes of wetland species. For example, the formation of adventitious roots, initiation of hypertrophied lenticels, and enhancement of aerenchyma tissue formation (Pezeshki, 2001). In this study, *H. anthelminthicus* developed adventitious roots at the beginning of the period, at week 4, while, *X. lanceatum* produced them later, at week 16. Hypertrophied lenticels, pores for exchange of gas, were not found in this study. The delay of adventitious root formation and lack of hypertrophied lenticels may affect growth and development of root and shoot in the flooded woody species. Many reports describe the importance of adventitious roots as the shoot growth supporter during prolonged flooding, especially in flood-tolerant species (Jackson, 1985; Armstrong et al., 1994; Islam and MacDonald, 2004; Pernot et al., 2019). Iwanaga and Yamamoto (2008) indicate the coincidental relationship between adventitious root formation and recovery of reduced photosynthetic rate in *Alnus japonica* under the water stress. Tsukahara and Kozlowski (1985) also report that height and diameter growth in flooded *Platanus occidentalis* seedlings decreased after removing adventitious roots from submerged portions of stem.

The current study showed that flooded *H. anthelminthicus* and *X. lanceatum* seedlings produced few adventitious roots with no effects on shoot growth. The function of adventitious roots in these species may play an important role in the growth and vitality of flooded seedlings. This could be investigated in future experiments of these two species by expanding study periods of flooding and various levels of submergences. Hypertrophied lenticels were not found in *H. anthelminthicus* and *X. lanceatum* seedlings under flooding condition during the study period. These lenticels were slowly developed in *Calophyllum longifolium* and *Virola surinamensis* during a flooding experiment, which resulted in root death and blocked the root growth (Lopez and Kursar, 1999). This indicates that the existence of adventitious roots and hypertrophied lenticels in response to flooding stress may present various effects depending on the species.

Extended flooding more than 12 weeks increased aboveground biomass and greatly decreased root:shoot ratio observed in *X. lanceatum* seedlings. It is possible that *X. lanceatum* seedlings escape the excessive water condition by elongating the stem length to obtain more oxygen and accumulate leaf biomass to enhance the photosynthetic efficiency to survive under flooding stress, an adaptive mechanism described by Yang and Li (2016) found in *Ptercarya stenoptera* and *Pinus elliottii* seedlings and Pires et al. (2018) found in *Genipa americana* from the dryland of Central Brazil. In addition, a decrease in biomass allocation to roots diminishes the metabolic requirement and stressed roots for oxygen, water and nutrient uptake (Naidoo and Naidoo, 1992).

5. CONCLUSIONS

Despite finding that flooding had negligible effects on growth in both *H. anthelminthicus* and *X. lanceatum*, further studies should focus on physiological and biochemical responses, which are easily induced through short-term soil flooding conditions, to provide more insights into constitutive adaptations of these species. In overall, our results indicated that *H. anthelminthicus* and *X. lanceatum* are considered to be flood-tolerant species because none of the seedlings had died by the end of the study. Therefore, both native species are promising candidates for the riparian restoration in this region.

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