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Effects of Waterlogging on Growth and Physiology of *Hopea odorata* Roxb

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Abstract

This study examines the growth and physiological characteristics of *Hopea odorata* growing under waterlogging condition. *H. odorata* was selected as it is widely planted as urban landscape tree species which experienced some growth stresses. Two waterlogging treatments and a control were designed. Forty 5-year old saplings each were subjected to waterlogged condition for 30 days which were then allowed to recover for a further 30 days as Treatment 1 (T1) and waterlogged condition for 60 days as Treatment 2 (T2). Aboveground and belowground biomass including leaf area was determined before and at 30 and 60 days of study. The net photosynthesis (A_{net}), stomatal conductance (Gs), transpiration rate per unit leaf area (E_L) and leaf to air vapour pressure deficit (ΔW) were assessed weekly for 60 days. The results showed that there were no significant differences between treatments for all growth attributes. There were also no significant effects were observed in gas exchange variables. The results demonstrate that severe waterlogged condition did not affect the physiology of *H. odorata*. These findings add to the increasing evidences that *H. odorata* is a flood as well as a pollution tolerance species that ensuring it to survive and grow well in urban areas by regulating the partitioning strategies.

Keywords: Waterlogging, Hopea odorata, Gas exchange, Growth, Physiology

1. Introduction

Urban forests can play a critical role in helping to reduce increasing levels of atmospheric CO_2 , as well as provide a wide variety of ecological services and amenities to communities. Trees store carbon (C) derived from CO_2 , the major gas contributing to global climate change, reduce peak cooling and heating loads on power plants, thereby reducing C emissions. They can also reduce the higher ambient air temperatures which occur in urbanized areas due to large amounts of heat-absorbing materials. However, plants planted in urban areas are frequently exposed to a variety of environmental stresses that occur concurrently. These compounding stresses can be more detrimental to plant growth and survival than either stress when encountered alone. The ability of a plant to resist stresses can be an important factor in plant growth and survival. Overall, the wide variety of stresses that plants are exposed to elicit relatively similar responses from plants (Lichtenhaler, 1996). However, when the stress is severe enough to overwhelm the preconditioned defense of the plant, long term damage can occur.

In urban areas, one of the common stresses is waterlogging. Waterlogging is defined as ponding of water over an area of crop land (Scott and Batchelor, 1979). It can be induced by an abundance of rainfall or supraoptimal irrigation, especially in areas where land is poorly leveled. Waterlogging reduces plant growth rate by replacing the soil's air with water, therefore depriving of oxygen in the roots. Since oxygen diffuses slower through water than air, the roots soon become deprived of oxygen which then unable to maintain normal respiration. Although several abnormalities result from this rapid oxygen deprivation by soil microbe, yield loss appears linked most closely to reduced nitrogen uptake (Bacanamwo and Purcell, 1999 and Kozlowski, 1984).

Plants become affected in a number of ways when soil becomes flooded. Air within the soil pore spaces has oxygen content similar to that of the atmosphere (about 20%) (Pezeshki, 1994). When soil becomes flooded, the ordinary air in the pore spaces of the soil is replaced with water, greatly restricting the flow of oxygen through the soil. The small amount of oxygen left in the soil is quickly depleted by root and soil microorganisms' respiration. Soil oxygen depletion is accelerated under warmer soil temperatures, because oxygen becomes less soluble in water as temperature rises. Pezeshki (1994) stated that once the soil becomes anaerobic, adverse effects on plants occur such as chlorosis, reduced growth rate, disruption of cell membranes, adverse effects on mineral uptake, altered growth regulator relationships, stomatal closure, leaf wilting and epinasty, reduced photosynthesis and respiration, altered carbohydrate partitioning, and potentially death. To date, with few exceptions (Thomson et al. 1992; Malik et al. 2001) most experiments investigating the effects of waterlogging on plant growth have evaluated responses during waterlogging, or, in cases when recovery was assessed, only the effects on final yield were considered (Watson et al. 1976; Belford et al. 1985; Meyer et al. 1985; Meyer & Barrs, 1988; Melhuish et al., 1991). Knowledge of the physiology of recovery after varying durations of waterlogging is scanty. Here, we assess the effects of waterlogging on growth and physiology caused by two durations of exposure and also the basis of recovery from this stress. The present study evaluates some growth attributes, and photosynthetic capacity and efficiency during waterlogging as well as during subsequent recovery when the soil was drained. The study attempts to examine the relative tolerance of an indigenous dipterocarp species, i.e Hopea odorata to waterlogging. H. odorata was chosen since it is widely planted as urban tree in Malaysia. Eventhough it originated from natural forest, this species seems to be adapted well in urban areas. In this paper, an attempt was made to explain a few mechanisms which the species utilize to tolerate or to avoid harmful effects of the applied stress.

2. Materials and methods

2.1 Plant materials and experimental design

A total of 60 saplings aged five years were obtained from Mantin Nursery, Negeri Sembilan, Malaysia. They were transplanted into 10-litre polyethylene bags potted with mixture of 2: 1: 1 of soil, peat and sand, and they were then supplied with slow-release fertilizer. These saplings were then divided into three groups (two treatment groups and a control). There were 20 saplings assigned to each treatment utilizing a Randomized Complete Block Design (RCBD) with two concrete frames sized 1 m X 4 m laid with high durable plastic sheets which were then filled to volume with water. Each frame was divided into six subframes and each subframe comprised of five saplings. Two replicates were assigned randomly for each treatment. The water was added and maintained periodically at 4 cm above the soil surface for waterlogged condition while saplings for the control subframe were being watered daily until the end of experiment.

2.2 Growth attributes measurement

Each treatment with five saplings were selected randomly and were then destructed in every time of measurements. The destructed saplings were divided into three parts, i.e. root, stem and branch (if any), and shoot (leaf). All the leaves were excised from the destructed saplings and total leaf area was determined using LI-3100 leaf area meter (LiCor Inc, Lincoln, Nebraska, USA). These leaves were then dried in an oven at 60°C for four days. Meanwhile, masses of the root and the stem were measured immediately after they were cleaned and oven dried at 70°C for four days or until constant weight was achieved.

2.3 Gas exchange measurement

The gas exchange measurement of all saplings was compared between treatments together with a control. The measurements were conducted on a random subframe-by-subframe basis on sunny days between 8:00 AM and 12:00 PM using LiCor 6400 portable photosynthesis system (LiCor Inc, Lincoln, Nebraska, USA) at initial stage and every week for duration of eight weeks. The gas exchange measurements were made on fully expanded leaves from the uppermost part of each sapling. Since the frames were placed under shading mesh, all plants were exposed to 15 minutes of full sunlight to allow for stomatal opening prior to taking measurements. The sample leaf was then placed in the cuvette that was maintained at 27° C and exposed to 1200μ mol.m .s PAR and CO₂ concentration was set to 360μ mol.m .s . Once stomatal conductance and CO₂ assimilation stabilized, data were recorded. When inside the cuvette, all sampled leaves were exposed to identical environmental conditions. Three sequential measurements were made within 1 to 4 minutes, and the average values were used for analyses.

2.4 Data analyses

The data obtained from repeated measurements were summed and averaged for each individual tree prior to any data analysis. If necessary, data transformations (normalised) were applied to stabilise error variance. These data were then analysed using one-way analysis of variance (ANOVA) and general linear model (GLM) for balanced and unbalanced data among treatments respectively. All the statistical analyses were performed using Statistical Analysis System version 9.0 (SAS Institute Inc. 2002) and the significance level was set at 0.05.

3. Results and discussion

3.1 Growth attributes

Table 1 shows the summary of ANOVA. There were no significant effects of waterlogging found between treatments for all the growth attributes taken. However, significant differences between treatments for all the parameters were only observed over time.

<<Insert Table 1 here>>

The mean values for all the growth attributes were plotted in Figure 1. Regardless of insignificant effects of waterlogging throughout the experimental period, the growing trends were observed in aboveground biomass ($M_{\text{stem+branch}}$ and M_{leaf}) as shown in Figure 1A and Figure 1C. In contrast, no growing trends were observed in belowground biomass (M_{root}) for all the treatments (Figure 1B). The growing trends of leaf area (A_L) were more apparent in T2 which is shown the highest value at 60 days (Figure 1D). In both waterlogging treatments, there were substantial increasing trends as compared to control.

<<Insert Figure 1 here>>

3.2 Gas exchange attributes

Similar results were also observed in gas exchange attributes. There were no significant differences between treatments and the interaction between treatment and time (Table 2) for net photosynthesis (A_{net}), stomatal conductance (Gs), transpiration rate per unit leaf area (E_L) and leaf to air vapour pressure deficit (ΔW). In contrast, significant differences were only found over time.

<<Insert Table 2>>

The mean values of each gas exchange parameter for every measurement were summarized in Figure 2. Similar trends were observed for A_{net} , Gs and E_L throughout the experimental period. The steep decreasing patterns observed in week 2 and 3 for A_{net} (Figure 2A) and Gs (Figure 2B) were associated with leaf to air vapour deficit (ΔW) as shown in Figure 2D.

Data on responses of this species to waterlogging is almost non-existent or new. The data with regard to stress available for this species were related to nutrient and water stresses (Siti Rubiah and Ahmad Husni 2007). Hence, we demonstrated here the responses of *H. odorata* within 60 days waterlogged by measuring growth and physiological attributes. In this study, insignificant effects of waterlogging on biomass or even on net photosynthesis rate (A_{net}), stomatal conductance (Gs) and transpiration rate per unit leaf area (E_L) were found. From this, the physiological variables were not changed dramatically and the changes were only associated with changes of leaf to air vapour pressure deficit (ΔW). However, the increasing trends were observed in aboveground parts for stem and branch ($M_{stem+branch}$), and leaf (M_{leaf}).

<<Insert Figure 2>>

The results clearly indicated that *H. odorata* can tolerate well with stress imposed by long term (60 days) waterlogging treatment through controlling the carbon partitioning. The regulation of allocation of carbon was more pronounced in aboveground in waterlogged saplings. The extent to which newly acquired carbon was allocated to the production of new leaf area and this has contributed to the growing of aboveground parts. The functional equilibrium model introduced by Thornley (1976) and Brouwer (1983) has successfully described how leaf area might be preferentially expanded under low irradiances. The allocation to leaf area is clearly a subset of more general problem such as stress imposed by low irradiance. This principle can also be applied in these findings. The strategies that imposed by this species to avoid severe damage by increasing leaf area and mass in 60 days immersed in the water. By taking the value of leaf area and leaf mass in this study, the specific leaf area (SLA) which is leaf area to leaf mass ratio also increased in T2. In contrast, the low watering treatment was effective in inducing similar adaptive morphological changes such as reduced SLA as reported by Grace and Russell (1977). Judging from substantial increasing patterns of leaf area and mass, the plants were forced to expand the leaf area and accumulate mass in leaves rather than in stems, branches or roots. This could be it strategies to drain the water from the bottom by increasing leaf area and mass. During the growth of plants, water is removed from the soil by transpiration. The rate of transpiration is proportional to the leaf area. Trees have a large leaf area and deep roots encouraging a high transpiration rate and the transpiration by plants helps to dry out soils.

During rain, water will infiltrate more readily into a dry soil and the removal of water by transpiration allows more water to enter soils during rain and this will reduce water runoff and lower flooding or waterlogging.

The adaptive responses of this species have brought it up to survive well in urban areas. The present study clearly demonstrated that the growth and photosynthesis rate or other gas exchange attributes of *H. odorata* were unaffected by waterlogging. Responses of *H. odorata* to waterlog were invariable, and to some extent it was unexpected. The tolerance of the *H. odorata* to short and long-term waterlogging was quite surprising. In particular, this species tried to avoid severe damage to its system or dying off by increasing the partitioning of carbon and dry weight to leaf. Judging from both growth and physiological aspects, the effects of waterlogging were only seen on the partitioning strategies as discussed above.

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F Value			
$M_{ m root}$	$M_{ m stem+branch}$	$M_{ m leaf}$	Total $A_{\rm L}$
0.125 ^{ns}	0.101 ^{ns}	1.288 ^{ns}	1.498 ^{ns}
0.317 ^{ns}	9.363***	2.566 ^{ns}	7.289**
0.506 ^{ns}	1.119 ^{ns}	0.721 ^{ns}	1.33 ^{ns}
	0.125 ^{ns} 0.317 ^{ns}	0.125 ^{ns} 0.101 ^{ns} 0.317 ^{ns} 9.363 ^{***}	$\begin{array}{cccc} 0.125^{\rm ns} & 0.101^{\rm ns} & 1.288^{\rm ns} \\ 0.317^{\rm ns} & 9.363^{***} & 2.566^{\rm ns} \end{array}$

Table 1. Analysis of variance (ANOVA) for growth characteristics of *H. odorata* exposed to waterlogging treatments.

Note: * significant difference at p<0.05

** significant difference at p<0.01

*** significant difference at p<0.001

^{ns} Not significant

Table 2. Analysis of variance (ANOVA) for gas exchange attributes of *H. odorata* exposed to waterlogging treatments.

	Parameter F value					
Source of Variation						
	$A_{ m net}$	Gs	$E_{ m L}$	ΔW		
	$(\mu mol CO_2.m^{-2}.s^{-1})$	$(mol H_2O.m^{-2}.s^{-1})$	$(\text{mmol H}_2\text{O.m}^{-2}.\text{s}^{-1})$	(kPa)		
Treatment	0.504 ^{ns}	1.076 ^{ns}	0.459 ^{ns}	1.006 ^{ns}		
Time	4.001***	4.429***	3.267**	10.539***		
Treatment x Time	1.033 ^{ns}	0.8 ^{ns}	0.632 ^{ns}	1.297 ^{ns}		

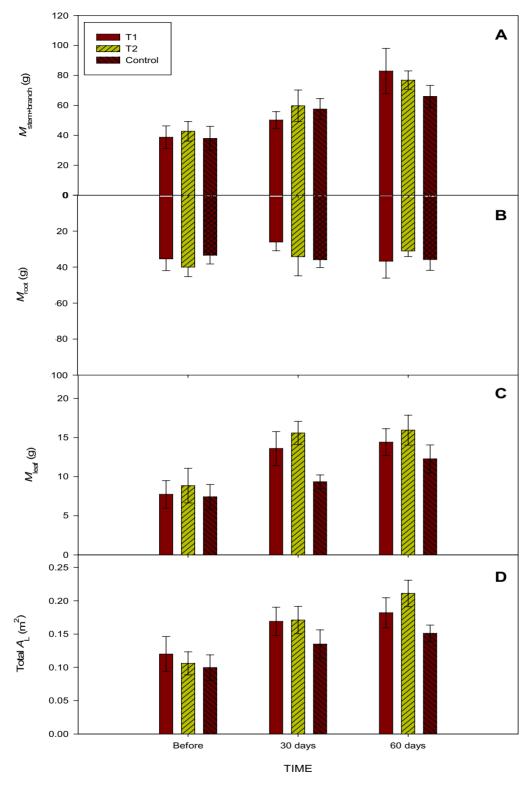


Figure 1. The mean values of stem and branch mass (A), root mass (B), leaf mass (C) and total leaf area (D) for each treatment.

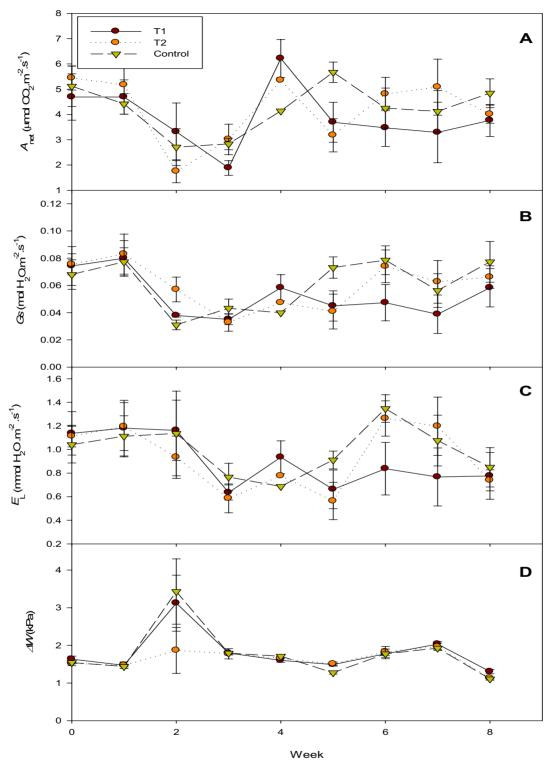


Figure 2. The mean values of net photosynthesis (A), stomatal conductance (B), transpiration rate per unit leaf area (C) and leaf to air vapour pressure deficit (D) for each treatment.