Growth of tamanu (*Calophyllum inophyllum* L.) seedlings in peat soil is inhibited by one week of flooding

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SUMMARY

Tamanu (*Calophyllum inophyllum* L.) has attracted increasing attention as a promising species for tropical peatland restoration in Southeast Asia. For successful restoration, it needs to survive and grow under flooded conditions, and flooding is a key factor affecting the performance of seedlings planted in tropical peatlands. To evaluate the restoration potential of tamanu, we examined the survival rate, plant height, number of leaves, root collar diameter, dry biomass and leaf area of tamanu seedlings grown in peat soil under different flooding durations, using a randomised block design. An experiment was conducted in a water tank using five flooding duration treatments and 12 tree-level replicates per treatment: F0 (non-flooding as control); F3 (3 days flooding); F5 (5 days flooding); F7 (7 days flooding); and F11 (11 days flooding). All seedlings survived across all treatments; however, their growth was inhibited as the flooding duration increased, particularly beyond one week. Of the performance indicators evaluated, number of leaves appeared to be the most sensitive to flooding stress, indicating its potential as an early indicator of plant stress. This study confirmed that even short-term flooding can cause significant growth reduction in *C. inophyllum* seedlings planted in tropical peat soils. Further studies are needed to reflect a wider range of flooding durations and water levels that may occur in tropical peatlands in the future.

KEY WORDS: flooding tolerance, restoration, revegetation, tropical peatland

INTRODUCTION

Tropical peatlands store one-sixth of the global peatland carbon pool (105 Gton) yet are threatened by deforestation, drainage, fire, conversion to agricultural land, and climate change (Page *et al.* 2022). The rate of carbon emission from degraded tropical peatlands can be double that from intact tropical peatlands (Deshmukh *et al.* 2021). Degraded tropical peatlands also suffer from land subsidence due to lower groundwater levels (Mishra *et al.* 2021, Yuwati *et al.* 2021), changes in hydrology and nutrient cycling, and an increased vulnerability to fire, which worsens the degradation (Syahza *et al.* 2020, Sofiyuddin *et al.* 2021). To avoid and alleviate these negative consequences, avoiding conversion and promoting restoration of tropical peatlands have been suggested as nature-based solutions for mitigating climate change (Strack *et al.* 2022, Tan *et al.* 2022, Yang *et al*. 2023). Asia accounts for about 38 % of the world's tropical peatlands, ranking second after South America (44 %) in both area and volume. Indonesia is the largest regional contributor to both the area and volume of tropical peatlands in Asia (Gumbricht *et al.* 2017). To protect and restore tropical peatlands in Indonesia, the Peatland Restoration Agency of the Government of Indonesia, known as Badan Restorasi Gambut (BRG), emphasised the 3Rs approach:

1. Rewetting of drained peatlands;
2. Revegetation of degraded peatlands; and
3. Revitalisation of local livelihoods relying on peatlands (President of the Republic of Indonesia 2016, Terzano *et al.* 2022).

This framework has continued to guide peatland restoration efforts even after the reorganisation of BRG into BRGM (Badan Restorasi Gambut dan Mangrove), its dissolution in 2025 and the subsequent transfer of restoration responsibilities to relevant ministries and local government (Raharjo *et al*. 2025).

Tree species that are commonly used for revegetation of tropical peatlands are *Shorea balangeran* and *Dyera polyphylla*, due to their adaptability to flooding stress (Smith *et al*. 2022). Another promising tree species for revegetation of tropical peatlands is *Calophyllum inophyllum* L., which is indigenous to Indonesia and notable in this context for its ecological ability to adapt to waterlogged conditions and the economic value of its seed oil (Maimunah *et al.* 2018, Leksono *et al.* 2022, Maulidya *et al.* 2024). *Calophyllum inophyllum* is commonly known as 'tamanu' and locally as 'nyamplung' (Dweek & Meadows 2002). It is an evergreen woody tree species found throughout the Western Ghats of India, tropical Asia, East Africa, Australia and a number of Pacific islands (Pawar & Patil 2019). It is distributed across many of the Indonesian islands including Java, Sumatra, Papua and the Nusa Tenggara Islands (Maimunah *et al.* 2018). Its seeds have very high oil content ranging from 50 % to 73 % of seed mass (Leksono *et al.* 2022, Fikri & Andrean 2023), and the seed oil can be used as a raw material in several high-value economic applications such as biofuels, cosmetics and traditional medicines (Adinugroho *et al.* 2019). Notably, the Ministry of Forestry of the Republic of Indonesia has highlighted that tamanu is a suitable species for biodiesel production, with a higher productivity (20 ton ha^{-1} yr^{-1}) than oil palm (6 ton ha^{-1} yr^{-1}) (Sanudin 2020, Fikri & Andrean 2023). On this basis, since 2017 the Centre for International Forestry Research and World Agroforestry (CIFOR-ICRAF) has focused on the potential of revegetation with tamanu as a restoration measure in experimental plantations on degraded tropical peatlands (CIFOR 2024). Even though the natural habitat of tamanu is land–sea transitional tropical forest ecosystems with mainly sandy soils on beaches (Vittaya *et al.* 2023), it has been known to exhibit some capacity for adaptation to waterlogged peat soil. For example, field-based research by Maimunah *et al.* (2018) showed that tamanu was the most adaptable of four tropical tree species tested, with a seedling survival rate of 88 % one year after planting on burned and degraded peatland in Central Kalimantan. Another field-based study reported a survival rate of more than 80 % for two-year-old tamanu in both ombrogenous peatland (i.e., higher than the surrounding land and receiving water only from precipitation) and topogenous peatland (i.e., directly above the mineral soil and affected by tidal water or river runoff) in Central Kalimantan (Leksono *et al.* 2022).

Peatlands in Indonesia are generally exposed to large variations in flooding duration, from short and frequent flooding (i.e., a few days) to long and occasional flooding (i.e., around six months) (Irfan *et al.* 2020, Khakim *et al.* 2022), especially during wet seasons. Flooding duration patterns usually reflect the dry and wet seasons in tropical regions, which are influenced by the variations in rainfall caused by climate phenomena (i.e., El Niño, La Niña, and positive or negative Indian Ocean Dipole) (Supari *et al.* 2018, Firmansyah *et al.* 2022, Iskandar *et al.* 2022); or they reflect anthropogenic interventions such as canal construction and blocking (Ritzema *et al.* 2014, Herawati *et al.* 2018). Since tree planting on Indonesian peatlands aims to restore peatlands that have been degraded by severe fires during dry seasons, tree seedlings are usually planted between the end of the dry season and beginning of the wet season (in September–October) to avoid fire (Irmawati, personal communication 2024). However, this makes the seedlings vulnerable to flooding during the wet season (Giesen 2004, Wibisono *et al*. 2005, van Eijk *et al*. 2009, Smith *et al*. 2022).

Only one recent experimental study, by Maulidya *et al.* (2024), has shed light on the effects of flooding level on the survival and growth of tamanu seedlings on peat soil. These authors reported that the survival rate was 100 % at all groundwater levels from –15 cm (below the soil surface) to 0 cm (at the soil surface), up to 81 days after sowing. However, compared to the fully drained control, growth was inhibited when the groundwater level was higher than –15 cm. Even though flooding duration, along with flooding depth, is one of the best explanatory factors for the survival rate, growth and distribution of trees (Kramer *et al.* 2008), there is little understanding of the survival rate and growth of tamanu seedlings under a range of flooding durations. Yang *et al*. (2025) reported that all tamanu seedlings planted to restore degraded peatlands in Perigi Village (South Sumatra, Indonesia) died when the flooding duration was abnormally prolonged to six months due to both La Niña and canal blocking in 2022. However, there has been little research on the effects of short flooding durations – lasting only a few days – on the survival and growth of tamanu seedlings in peat soil.

Facilitating the initial growth of tamanu seedlings for tropical peatland restoration requires an improved understanding of their responses to flooding durations. Therefore, we aimed to investigate the survival rates and growth performances of tamanu seedlings under short-term flooding durations in peat soil under controlled conditions in a water tank. We hypothesised that the seedling survival rate of tamanu, a species known to be highly adaptive to waterlogged conditions, is not negatively affected by flooding of short duration, but the growth (i.e., plant height, number of leaves, root collar diameter, dry biomass and leaf area) is inhibited by even a few days of flooding. We anticipate that our results can help to develop an easy and applicable guideline for tropical peatland revegetation using tamanu seedlings.

METHODS

The experiment was conducted in a plant nursery and a water tank at the Department of Agricultural Cultivation, Faculty of Agriculture, Sriwijaya University, South Sumatra Province, Indonesia (3° 13′ 12.30″ S, 104° 38′ 50.70″ E), from August to November 2018. At the study site in 2018, annual mean air temperature was 30.7 ± 1.0 °C (mean ± standard deviation); mean monthly precipitation was 48.1 ± 30.7 mm month^{-1} during the dry season (June–October) and 175.2 ± 59 mm month^{-1} during the wet season (November–May); and monthly mean relative humidity was 74.3 ± 6.8 % during the dry season and 83.6 ± 2.0 % during the wet season (BMKG 2018).

Peat for use as the planting medium was collected from a tropical peatland (3° 13′ 26.60″ S, 104° 38′ 47.10″ E) near the Indralaya campus of Sriwijaya University and transported to the nursery in a cooling box. The peat soil was first cleaned of large litter and insects and then placed in cylindrical polyethylene bags (polybags). The polybags were 25 cm in height and 14 cm in diameter, and they were filled with peat soil to 20 cm height (5 cm below their tops). Each polybag had a bottom hole and side holes which facilitated water movement in and out of the polybag, allowing us to investigate the effect of different flooding duration treatments on the survival and growth of seedlings. We dissolved 10 g of fungicide (Antracol, Bayer CropScience, Jakarta, Indonesia) in 1 L of water and added 200 mL of the solution per polybag to protect the peat soil from microorganisms. Tamanu seeds were collected in Lombok, Nusa Tenggara Barat, Indonesia (8° 33′ 54.00″ S, 116° 21′ 3.60″ E) in June 2018, and were transported to the nursery in dark and cooled containers.

Before sowing, we selected healthy tamanu seeds with broken hard shells and ivory colouring. We sowed the seeds with one-third buried in the peat soil and the rest exposed to the air. During germination and initial growth (before the flooding duration treatments), the seedlings were kept in the nursery for 40 days to achieve the minimum growth stage for outplanting (Maulidya *et al.* 2024), with watering once every three days with 200 mL of tap water per polybag, which prevented the peat soil from drying out. Fertilisation was carried out 30 days after sowing (DAS) using NPK fertiliser with concentrations of 16 % nitrogen, phosphorus and potassium at a rate of 3 g per polybag (Leksono *et al*. 2014, Maulidya *et al*. 2024).

The experiment used a randomised block design. After 40 DAS, the flooding duration treatments were carried out in the water tank. The water tank was equipped with a transparent rain shield and designed with uneven floor levels, allowing some seedlings to be submerged while others remained unflooded when water was added (Figure 1). A drainage outlet was installed in the tank and used to adjust water levels or replace the water in the tank. A total of 60 seedlings

Figure 1. *Calophyllum inophyllum* seedlings under different flooding duration treatments in the water tank.

(= 5 flooding duration treatments × 12 tree-level replicates) were used for the experiment. The flooding duration treatment consisted of F0 (non-flooding as control); F3 (3 days flooding); F5 (5 days flooding); F7 (7 days flooding); and F11 (11 days flooding). During the experiment, the F0 seedlings were watered once every three days with 200 mL of tap water per polybag to prevent them from drying out, and carefully managed to prevent any exposure to flooding. At the same time, the flooding levels of F3, F5, F7 and F11 were carefully managed (manually) every day to ensure flooding to 5 cm above the soil surface. The water in the tank was replaced every five days to maintain clean conditions. At each replacement, the water level was carefully adjusted to ensure that the planned flooding duration treatments were consistently maintained. After each flooding duration treatment was finished, the F3, F5, F7 and F11 seedlings were managed in the same way as F0 until 81 DAS.

We measured the survival rate, plant height, number of leaves and root collar diameter (i.e., stem diameter at soil surface) eight times (i.e., immediately before the flooding duration treatments = 40 DAS; immediately after each flooding duration treatment = 43, 45, 47 and 51 DAS; 10, 20 and 30 days after the final treatment = 61, 71 and 81 DAS). We measured dry biomass and leaf area only once (at 81 DAS) for all 60 seedlings. All seedlings were harvested after 81 days for final measurements. The root collar diameters were measured at the soil surface with a Vernier caliper. Leaf area was measured using millimetre-squared graph paper. Specific leaf area was calculated as the quotient of total leaf area and leaf dry biomass. For dry biomass measurements the harvested plants were divided into organs (i.e., leaf, stem and root) and dried at 80 °C for 72 hours. The relative growth rates (RGR) of plant height, number of leaves and root collar diameter were calculated using the following equations (Hoffmann & Poorter 2002):

$$RGRH = (\ln H2 - \ln H1) / (t2 - t1) \quad [1]$$

$$RGRL = (\ln L2 - \ln L1) / (t2 - t1) \quad [2]$$

$$RGRD = (\ln D2 - \ln D1) / (t2 - t1) \quad [3]$$

where $RGRH$ is relative growth rate of plant height, $RGRL$ is relative growth rate of the number of leaves, and $RGRD$ is relative growth rate of root collar diameter; t_1 is the time of prior measurement, t_2 is the time of next measurement; $H1$ and $H2$ are plant heights at $t1$ and $t2$; $L1$ and $L2$ are the numbers of leaves at $t1$ and $t2$; and $D1$ and $D2$ are the root collar diameters at $t1$ and $t2$, respectively.

An aligned rank transformation ANOVA – a non-parametric approach to two-way ANOVA – was used to analyse plant height, number of leaves, root collar diameter and their relative growth rates due to violation of normality assumption (Leys & Schumann 2010, Wobbrock *et al.* 2011). We used ‘ARTool’ library for the test, followed by a post-hoc test with ‘art.con’ function. Other metrics such as dry biomass and biomass allocation to each organ harvested at 81 DAS, which satisfied the assumptions of normality and homogeneity of variance, were analysed using a one-way ANOVA followed by a Tukey’s post-hoc test. In contrast, leaf area and specific leaf area were analysed using a Kruskal-Wallis test due to a violation of normality assumption. The values were considered significantly different at $p < 0.05$. All statistical analyses were performed using R v4.3.2 (R Development Core Team 2014).

RESULTS

Survival rate

All tamanu seedlings survived for the full duration of all flooding treatments, providing enough replicates for plant height, number of leaves, root collar diameter, dry biomass and leaf area.

Growth performance

The results of the aligned rank transformation ANOVA and a one-way ANOVA on the effects of flooding duration (control, 3, 5, 7, 11 days flooding) and time (40, 43, 45, 47, 51, 61, 71, 81 DAS) on the growth performance are summarised in Table 1.

Plant height

Figure 2 illustrates the logistic growth of plant height from 40 to 81 DAS. For all flooding duration treatments, the initial growth of plant height was relatively rapid from 40 to 47 DAS, compared to the remaining period. At 40 DAS, plant heights did not differ significantly among treatments, with an overall mean of 14.7 ± 2.4 cm (mean ± standard deviation). However, the plant height of F0 increased rapidly from 51 DAS onward and became the highest (21.0 ± 3.6 cm) at 81 DAS, which was significantly higher than that of F11 (16.0 ± 2.8 cm). Other treatments, especially F11, grew more slowly compared to F0 during the whole period ($p < 0.05$ at all time points). Table 2 shows the relative growth rates of plant height ($RGRH$). $RGRH$ showed a clear decreasing trend as time passed. Between 51 and 61 DAS, $RGRH$ for F0 was significantly higher than for F5, F7 and F11. However, the statistical difference subsequently disappeared because the $RGRH$ for every treatment converged between 71 and 81 DAS.

Number of leaves

Figure 3 shows changes in the number of leaves from 40 to 81 DAS under different flooding durations. The initial numbers of leaves for all flooding duration treatments were not significantly different (count 7.6 ± 1.0). Until 47 DAS, there was no noticeable change across all treatments. However, the number of leaves in F0 increased rapidly following 51 DAS whereas the growth in number of leaves was inhibited until 51 DAS for F3 and F5, and until 61 DAS for F7 and F11. F5 and F11 even exhibited yellowing and loss of leaves. As a result, the number of leaves at 81 DAS was significantly higher in F0 (12.6 ± 2.2) than in other treatments (all $p < 0.05$). Table 3 shows the relative growth rates of the number of leaves ($RGRL$). The $RGRL$ values for all treatments fluctuated widely between 40 and 51 DAS. However, the fluctuations became smaller as time passed, and the $RGRL$ values per treatment converged close to zero between 71 and 81 DAS, with no significant differences.

Root collar diameter

Figure 4 illustrates the constant increase of root collar diameter from 40 to 80 DAS. At 40 DAS, root collar diameter did not differ significantly among treatments, with an overall mean of 2.8 ± 0.4 mm. All treatments showed relatively rapid growth of root collar diameter until 47 DAS, compared to the remaining period. The root collar diameter of F0 was constantly highest from 51 DAS and it was significantly higher (4.4 ± 0.4 mm) than that of F11 (3.7 ± 0.6 mm) at 81 DAS. Table 4 summarises the relative growth rates of root collar diameter ($RGRD$). Similar to the result for plant height, $RGRD$ decreased as time passed and converged at 81 DAS. Significant differences among treatments were not found during the whole period.

Table 1. Summaries of aligned rank transformation ANOVA and one-way ANOVA on the effects of time (40, 43, 45, 47, 51, 61, 71, 81 days after sowing) and flooding duration (control = 0, 3, 5, 7, 11 days) on the growth performance of *Calophyllum inophyllum*.

Metric	Factors	d.f.	F	p-value
Plant height	Time	7	12.32	< 0.001
	Flooding duration	4	18.43	< 0.001
	Time × Flooding duration	28	0.26	0.990
Number of leaves	Time	7	26.90	< 0.001
	Flooding duration	4	17.08	< 0.001
	Time × Flooding duration	28	1.76	< 0.050
Root collar diameter	Time	7	113.00	< 0.001
	Flooding duration	4	17.46	< 0.001
	Time × Flooding duration	28	1.36	0.110
Dry biomass	Flooding duration	4	3.33	< 0.050
Leaf area	Flooding duration	4	3.24	0.060
Specific leaf area	Flooding duration	4	2.77	0.090

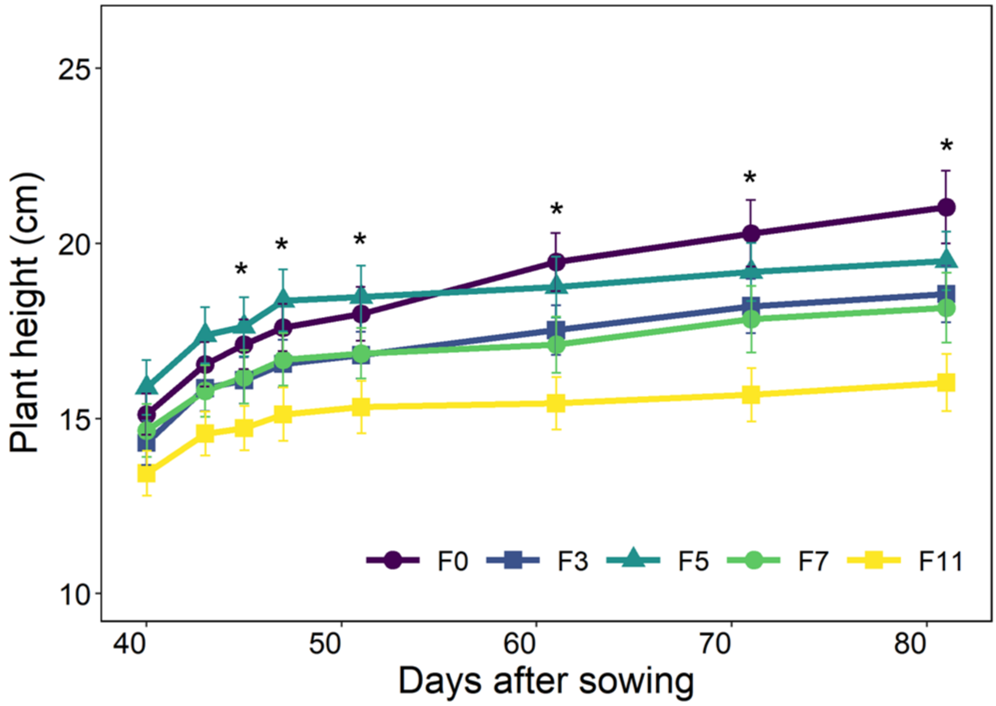

Figure 2. Plant height of tamanu seedlings under different flooding duration treatments 40–81 days after sowing. F0 indicates non-flooding as control; F3 means 3 days flooding; F5 indicates 5 days flooding; F7 means 7 days flooding; and F11 indicates 11 days flooding. The bars represent the standard error, and asterisks indicate significant differences ($p < 0.05$) among treatments.

Table 2. Relative growth rates of plant height (cm day^{-1}) under different flooding duration treatments 40–81 days after sowing. The values shown are means ± standard deviations. Different letters indicate statistically significant differences at $p < 0.05$.

Flooding duration	Relative growth rates of plant height (cm day^{-1})			
	40–43 DAS	43–45 DAS	45–47 DAS	47–51 DAS
F0 (control)	0.030±0.008 a	0.016±0.020 a	0.014±0.012 a	0.005±0.007 a
F3 (3 days)	0.035±0.018 a	0.007±0.010 a	0.014±0.010 a	0.004±0.003 a
F5 (5 days)	0.030±0.012 a	0.007±0.010 a	0.021±0.015 a	0.001±0.002 a
F7 (7 days)	0.026±0.012 a	0.012±0.010 a	0.016±0.024 a	0.003±0.004 a
F11 (11 days)	0.028±0.015 a	0.005±0.010 a	0.011±0.021 a	0.004±0.007 a

Flooding duration	Relative growth rates of plant height (cm day^{-1})		
	51–61 DAS	61–71 DAS	71–81 DAS
F0 (control)	0.008±0.005 a	0.004±0.003 a	0.003±0.004 a
F3 (3 days)	0.004±0.002 ab	0.004±0.004 a	0.002±0.002 a
F5 (5 days)	0.002±0.002 bc	0.002±0.003 a	0.002±0.001 a
F7 (7 days)	0.001±0.002 bc	0.004±0.004 a	0.002±0.002 a
F11 (11 days)	0.001±0.003 c	0.002±0.006 a	0.002±0.004 a

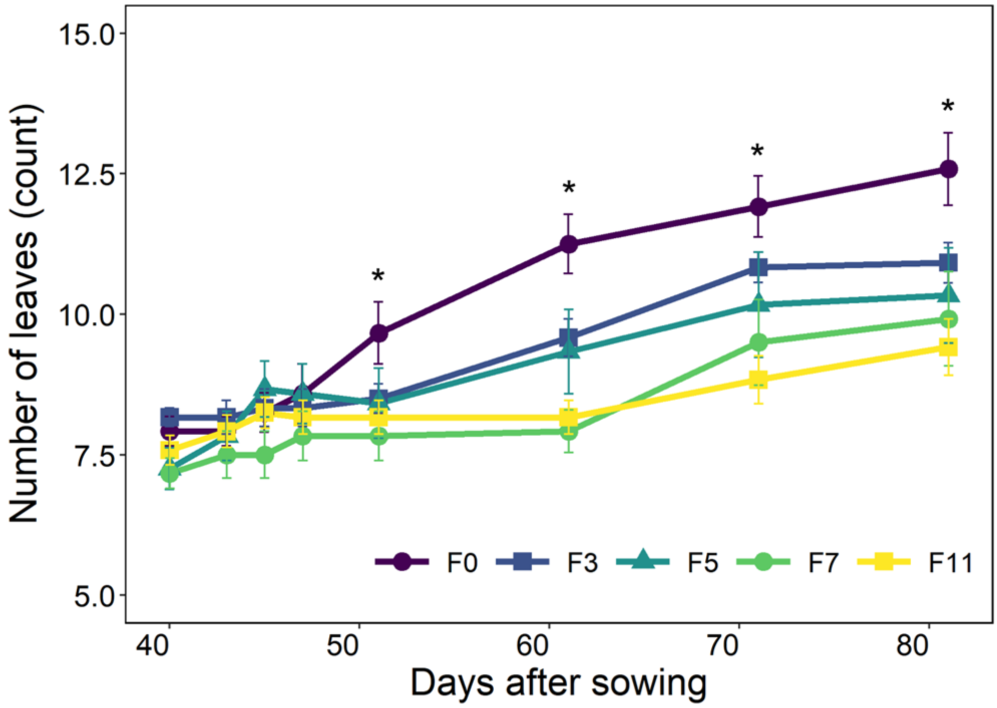

Figure 3. Number of leaves of tamanu seedlings under different flooding duration treatments 40–81 days after sowing. F0 indicates non-flooding as control; F3 means 3 days flooding; F5 indicates 5 days flooding; F7 means 7 days flooding; and F11 indicates 11 days flooding. The bars represent the standard error, and asterisks indicate significant differences ($p < 0.05$) among treatments.

Table 3. Relative growth rates of number of leaves (count day^{-1}) under different flooding duration treatments 40–81 days after sowing. The values shown are means ± standard deviations. Different letters indicate statistically significant differences at $p < 0.05$.

Flooding duration	Relative growth rates of number of leaves (count day^{-1})			
	40–43 DAS	43–45 DAS	45–47 DAS	47–51 DAS
F0 (control)	0.000±0.000 a	0.019±0.042 a	0.015±0.034 a	0.030±0.043 a
F3 (3 days)	−0.002±0.035 a	0.009±0.031 a	0.000±0.000 a	0.006±0.020 ab
F5 (5 days)	0.026±0.049 a	0.050±0.061 a	−0.006±0.021 a	−0.008±0.028 b
F7 (7 days)	0.012±0.028 a	0.000±0.000 a	0.021±0.047 a	0.000±0.000 b
F11 (11 days)	0.014±0.032 a	0.021±0.048 a	−0.006±0.049 a	0.000±0.000 b

Flooding duration	Relative growth rates of number of leaves (count day^{-1})		
	51–61 DAS	61–71 DAS	71–81 DAS
F0 (control)	0.016±0.015 a	0.006±0.008 a	0.005±0.008 a
F3 (3 days)	0.012±0.013 ab	0.013±0.013 a	0.001±0.006 a
F5 (5 days)	0.009±0.010 ab	0.007±0.013 a	0.003±0.011 a
F7 (7 days)	0.002±0.012 ab	0.016±0.016 a	0.004±0.009 a
F11 (11 days)	0.000±0.000 b	0.007±0.013 a	0.006±0.009 a

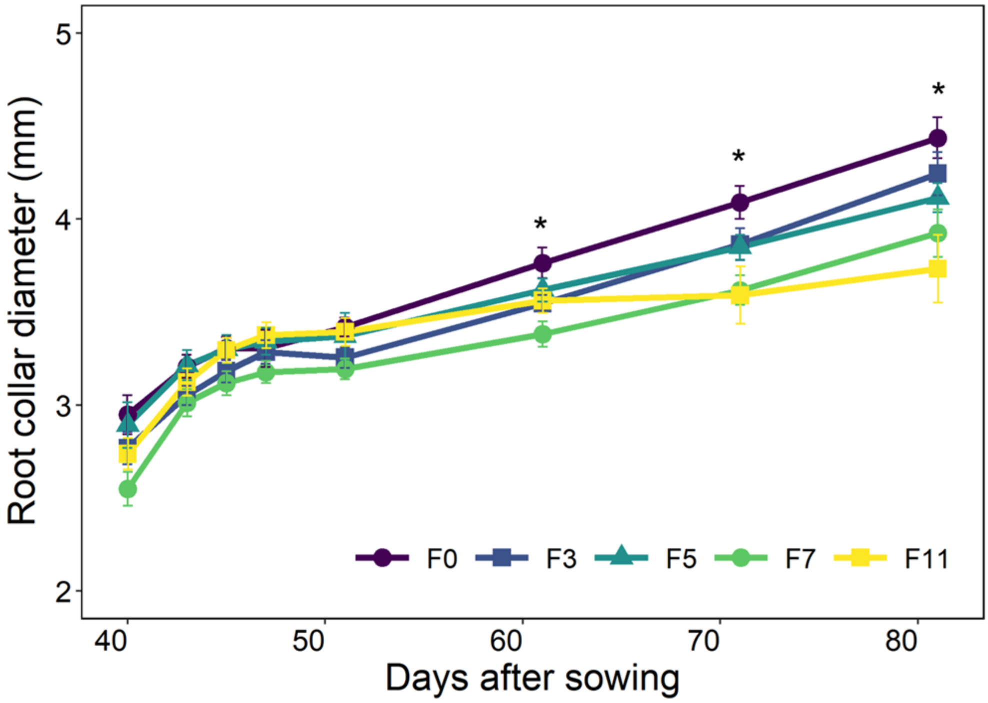

Figure 4. Root collar diameter of tamanu seedlings under different flooding duration treatments 40–81 days after sowing. F0 indicates non-flooding as control; F3 means 3 days flooding; F5 indicates 5 days flooding; F7 means 7 days flooding; and F11 indicates 11 days flooding. The bars represent the standard error, and asterisks indicate significant differences ($p < 0.05$) among treatments.

Table 4. Relative growth rates of root collar diameter (mm day^{-1}) under different flooding duration treatments 40–81 days after sowing. The values shown are means ± standard deviations. Different letters indicate statistically significant differences at $p < 0.05$.

Flooding duration	Relative growth rates of root collar diameter (mm day^{-1})			
	40–43 DAS	43–45 DAS	45–47 DAS	47–51 DAS
F0 (control)	0.030±0.029 a	0.015±0.011 a	−0.002±0.046 a	0.010±0.024 a
F3 (3 days)	0.034±0.032 a	0.021±0.015 a	0.016±0.015 a	−0.002±0.014 a
F5 (5 days)	0.037±0.038 a	0.014±0.015 a	0.006±0.008 a	0.001±0.034 a
F7 (7 days)	0.057±0.049 a	0.018±0.030 a	0.010±0.008 a	0.001±0.003 a
F11 (11 days)	0.045±0.039 a	0.027±0.029 a	0.012±0.006 a	0.001±0.003 a

Flooding duration	Relative growth rates of root collar diameter (mm day^{-1})		
	51–61 DAS	61–71 DAS	71–81 DAS
F0 (control)	0.009±0.006 a	0.008±0.003 a	0.008±0.003 a
F3 (3 days)	0.009±0.005 a	0.008±0.006 a	0.009±0.007 a
F5 (5 days)	0.008±0.011 a	0.006±0.003 a	0.007±0.003 a
F7 (7 days)	0.006±0.004 a	0.007±0.005 a	0.008±0.006 a
F11 (11 days)	0.005±0.005 a	0.000±0.013 a	0.004±0.006 a

Dry biomass

The effect of flooding duration treatment on plant dry biomass (roots, stems and leaves) at 81 DAS can be seen in Figure 5a. Although differences were not significant, in general the leaf, root and stem biomass were highest in F0 and showed decreasing trends to F11 (Figure 5a). As a result, the total dry biomass was significantly higher in F0 (12.31 ± 0.88 g) than in F7 (7.06 ± 1.93 g) and F11 (7.07 ± 0.96 g) (all $p < 0.05$). Although the biomass allocation did not differ significantly among the flooding durations, seedlings under flooding stress tended to allocate more biomass to roots and leaves, whereas those grown under non-stress conditions invested more in stem growth (Figure 5b).

Leaf area and specific leaf area

Figure 6 shows the leaf area and specific leaf area at 81 DAS under the different flooding duration treatments. As expected, the leaf area was greatest in F0 (361.70 ± 122.63 cm^2) although differences were not significant. As a result, the specific leaf area was highest in F0 and lowest in F11, but differences were again not significant.

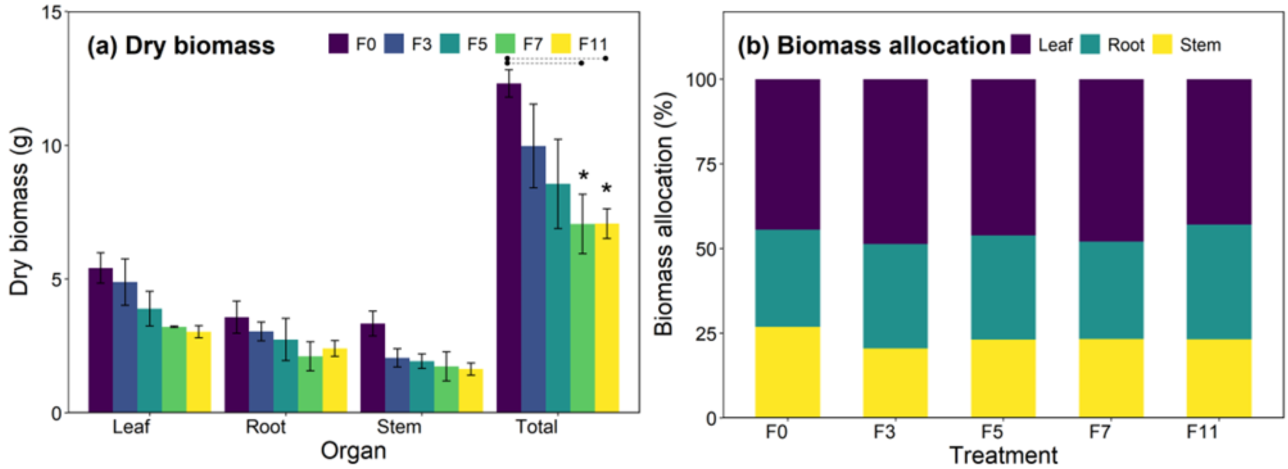

Figure 5. (a) Dry biomass and (b) biomass allocation of tamanu seedlings under different flooding duration treatments, at 81 days after sowing. F0 indicates non-flooding as control; F3 means 3 days flooding; F5 indicates 5 days flooding; F7 means 7 days flooding; and F11 indicates 11 days flooding. The bars represent the standard error, and asterisks indicate significant differences ($p < 0.05$) among treatments.

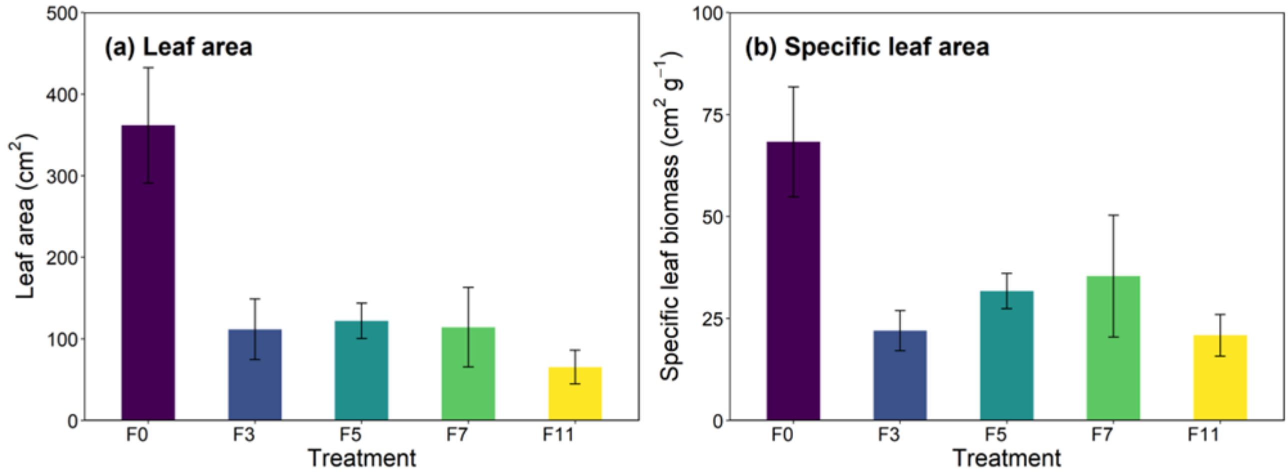

Figure 6. (a) Leaf area and (b) specific leaf area of tamanu seedlings under different flooding duration treatments, at 81 days after sowing. F0 indicates non-flooding as control; F3 means 3 days flooding; F5 indicates 5 days flooding; F7 means 7 days flooding; and F11 indicates 11 days flooding. The bars represent the standard error.

DISCUSSION

All of the tamanu seedlings survived eleven days of flooding during early development, although their growth was negatively affected when the flooding duration was longer than one week. Plant height and root collar diameter at eleven days were lower in the longest flooding treatment (F11, 11 days) than in the non-flooding treatment (F0), but did not show significant differences compared to the shorter flooding duration treatments. In contrast, the number of leaves was substantially reduced in all flooding duration treatments (F3, F5, F7, F11) compared to the non-flooding treatment (F0). Total dry biomass was significantly reduced when the flooding duration was longer than a week (F7, F11) compared to shorter flooding duration treatments. Thus, our results support the hypothesis that survival rates were not negatively affected at all, but growth was reduced, by a short-term flooding duration of about one week during the nursery stage.

Other flooding-tolerant species exhibit similar patterns even under longer flooding durations. For example, all seedlings of the southern neotropical swamp tree *Citronella gongonha* (Mart.) R.A.Howard survived for 120 days after flooding to 2 cm above the soil surface by developing morphological adaptations, but growth was impaired under longer-term flooding (Duarte *et al.* 2020). *Calophyllum brasiliense* Camb, which belongs to the same genus as tamanu and is known as a flooding tolerant species, also survived flooding; however, plant height and leaf production were substantially reduced under flooded conditions, particularly with longer flooding durations up to 150 days (de Oliveira & Joly 2010). Seedlings of two Amazonian trees, *Genipa americana* L. and *Guazuma ulmifolia* Lam. (Malvaceae), survived 30 days of flooding; however, their biomass was significantly reduced if submerged (Pires *et al.* 2018). The stunted growth of seedlings can be explained by the common responses to soil flooding stress. Under soil flooding, the availability of oxygen is reduced and elements that are toxic to plants accumulate (Frye & Grosse 1992, Colmer 2003). As a result, stomata are closed and pigments are degraded, leading to a decrease in photosynthetic capacity during flooding (Pezeshki 2001, de Oliveira & Joly 2010). Many plants survive under flooded conditions by reducing metabolism and saving energy via decreasing total biomass (Voesenek & Bailey-Serres 2015, Duarte *et al.* 2020). Based on our results, tamanu seedlings appear to do the same. However, it should also be carefully considered that seedling survival may decline with prolonged flooding duration, depending on the species, and particularly when flooding occurs at planting rather than at the nursery stage (Smith *et al*. 2022, Santosa *et al*. 2014, Tata *et al*. 2022, Harrison *et al*. 2023).

An interesting point is the differences in sensitivity of the growth metrics. Inhibition (and even loss) of leaves occurred under even the shortest flooding duration, whereas plant height and especially root collar diameter were less sensitive to flooding. As a result, leaf area also showed a large difference between the non-flooding and flooding duration treatments (Figure 5). These results align with the findings of Kroschel & King (2021) in an investigation of the seedlings of six temperate floodplain forest species (*Quercus lyrate*, *Q. texana*, *Q. phellos*, *Celtis laevigata*, *Fraxinus pennsylvanica* and *Ulmus americana*) under different flood durations. They found that a reduction in number of leaves was the most consistent change across all species and all flooding durations, while stem diameter showed little variation across all species. Maulidya *et al.* (2024) and Norsamsi *et al*. (2015) also reported that the leaf area of tamanu decreased substantially in soil flooding conditions, while the growth of plant height and root collar diameter were maintained during the same period. Rood *et al.* (2010) explained that leaf loss and reduction of leaf area under flooded conditions represents a decrease in transpiration and photosynthetic surface area, which can cause a further decrease in energy gain. This result indicates that, in the case of tamanu seedlings, leaf loss is an initial expression of the stress introduced by flooding.

Although the biomass allocation of tamanu was not statistically significant, seedlings under flooding stress showed a slight morphological adaptation by allocating more biomass to roots and leaves than to stems. On the other hand, no flooding-adaptive structures such as hypertrophied lenticels or adventitious roots were observed in this study. Hypertrophied lenticels are enlarged cracks on the surfaces of stems and roots formed by hypertrophy of secondary aerenchyma. Aerenchyma can be exposed directly to the atmosphere through the lenticels, and thus admit oxygen from the air into the tree. Hypertrophied lenticels are thought to facilitate the release of other atmospheric gases from the tree trunk (Shimamura *et al.* 2010, Provost *et al.* 2016), which is a well-known adaptive strategy to soil flooding. Another organ associated with flood tolerance, the adventitious root, emerges from stem nodes and functions in the uptake of nitrogen and phosphorus from floodwater (Lin *et al*. 2023). According to Norsamsi *et al.* (2015), the number of individual tamanu seedlings developing hypertrophied lenticels was 20 % at 0 cm flooding depth and 60 % at 4 cm flooding depth after 30 days of flooding. *C. brasiliense* also developed hypertrophied lenticels on submerged parts of stems during the first week of flooding but rarely made adventitious roots (de Oliveira & Joly 2010). Generally, hypertrophied lenticels appeared more frequently than adventitious roots (Meli *et al.* 2021). It seems probable that clear morphological adaptations were not observable in our study of tamanu seedlings because the range of flooding duration treatments was relatively short.

Our results indicate that, to ensure rapid initial growth for tropical peatland revegetation with tamanu seedlings, inundation lasting more than a week should be avoided. Further investigation is warranted, as the survival and growth responses may differ not only between seedling and adult stages (Parolin *et al.* 2010) but also between nursery and outplanting phases (Harrison *et al*. 2023). According to Harrison *et al*. (2023), the nursery phase may serve as an opportunity to harden seedlings by exposing them early to flooding stress.

Considering the tree-planting period for Indonesia, from the end of the dry season to the beginning of the wet season to avoid fire risk in general, we suggest the appropriate times for planting tamanu are:

(1) at the end of a dry season, when the amount of rainfall decreases and the groundwater level becomes lower without inundation, while ensuring reduced risk of fire through effective management for fire prevention; and

(2) at the beginning of a wet season, planting on soil mounds to avoid flooding. Furthermore, monitoring leaf fall in the field can serve as an effective early indicator of flooding stress in tamanu seedlings.

The limitation of this study is that there were no signs of mortality, indicating that the flooding durations tested were too short to capture the full variability among the studied factors. Therefore, this study should be extended to longer flooding durations and various water levels reflecting real conditions in Indonesia's peatlands. In addition, comparing species-specific responses under the different hydrological conditions is required to underpin species selection for tropical peatland restoration. Further studies are under way to consider a wide range of flooding durations and depths across several tropical tree species. It is expected that this will enable us to identify the maximum flooding duration and depth that key restoration species can tolerate, thereby providing practical guidelines for the maintenance and management of restored tropical peat swamp forests.

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AUTHOR CONTRIBUTIONS

Conceptualisation: RAS; methodology: RAS, HY; software: RAS, HY; validation: HY, YF, RAS; investigation: YF, RAS; resources: DPP, EC; data curation: DPP, IW, HY; writing - preparation of original draft: RAS, YF, IW, HY, EC; writing - review and editing: HY, EC, IW, RAS; visualisation: YF, IW, HY; supervision: HY, RAS; project administration: EC, RAS; funding acquisition: EC. All authors have read and agreed to the published version of the manuscript.

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