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RESEARCH ARTICLE

Evaluating the combined effects of light and water availability on the early growth and physiology of *Tamarindus indica*: Implications for restoration

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Abstract

Premise: The tamarind tree (*Tamarindus indica*) is a species of significant cultural, economic, and ecological value, with a pantropical distribution. However, the tamarind is experiencing a decline in wild populations in its native range, but the reasons for its decline remain unknown.

Methods: We examined the critical early life-history stages for tamarind establishment to understand how varying levels of light and water availability and watering frequency affect its regeneration. Through three greenhouse experiments, we assessed the impact of these resources on the germination, survival, growth, and physiological responses of tamarind seedlings and saplings.

Results: Water availability was critical for seed germination, but not light levels or pre-germination treatments. Light was the primary limiting factor for seedling growth. Tamarinds in high light availability grew taller, had more biomass and larger diameter, but the effect of light was modulated by water availability, indicating that there was an interaction between both resources. Water and light affected specific leaf area and leaf dry matter content but not biomass allocation, root-to-shoot ratio, or stomatal conductance. Water availability influenced sapling growth, but watering frequency did not, indicating a resilience of tamarind saplings to changes in rainfall periodicity but a sensitivity to total rainfall amounts.

Conclusions: Our study underscores the importance of considering both light and water availability in tamarind restoration efforts and contribute to understanding plant responses and trade-offs under different levels of critical resources. Our findings will inform conservation strategies to support the regeneration and long-term survival of *Tamarindus indica* in its native habitats.

KEYWORDS

Fabaceae, light, resource availability, restoration, seed germination, seedling growth, *Tamarindus indica*, trade-off hypothesis, watering frequency

Tamarindus indica L. (Fabaceae), commonly known as the tamarind tree, is a culturally, economically, and ecologically important species around the world. Its origins can be traced back to Africa, but tamarinds are now cultivated throughout the tropics in over 50 countries (El-Siddig et al., 2006; Diallo et al., 2007). In its native range, particularly in dry and semiarid regions, tamarind trees are immensely important for humans and non-human communities alike, with significant roles in cultural traditions, and provide valuable nutrition during famines (Van Der Stege et al., 2011; Ranaivoson et al., 2015). In Madagascar, for example, tamarind is a keystone species for lemurs, contributing up to 70% of their diet during specific times of the year (Simmen et al., 2003). Although it is widely cultivated on farms, studies from countries including Madagascar, Niger, Sudan, Nigeria, Kenya, and Benin have reported that wild populations of tamarind are declining in the native range (Muhammad and Amusa, 2003; Blumenfeld-Jones et al., 2006; Fandohan et al., 2010; Soumana et al., 2010; Nyadoi et al., 2011; Ranaivoson et al., 2015; Garba et al., 2020; Mohammed et al., 2021; Samarou et al., 2022). Studies on these populations consistently show that regeneration is very low or nonexistent, raising concerns about the long-term survival of tamarinds in the wild and the potential consequences for other species that depend on it.

The underlying causes of the decline of wild tamarind populations remain unknown. Some studies emphasize high seedling mortality (Winchester et al., 2018). Other postulated causes include the lack of factors required to break dormancy, allelopathic effects of adult tamarind trees inhibiting growth, low water availability in the soil, and the impact of anthropogenic activities such as pod harvesting (Muhammad and Amusa, 2003; Blumenfeld-Jones et al., 2006; Mertl-Millhollen et al., 2011). Notably, studies reporting a decline in wild tamarind populations share a commonality: They were conducted in arid areas where wild tamarind populations are vulnerable, especially in habitats facing higher human pressure and drought stress. Consequently, it is challenging to separate the impact of droughts from human pressures. The looming threat of climate change, characterized by alterations to rainfall patterns and increased drought frequency, poses a significant risk to species like the tamarind (Malhi and Wright, 2004). Future climate scenarios predict prolonged drought periods (Dai, 2011; Feldman et al., 2024), adding urgency to understanding how water availability affects tamarind populations and their requirements for seed germination and seedling establishment in the wild.

Tamarinds are naturally found in dry areas, where they are often described as drought resistant in their adult stage (El-Siddig et al., 2006), but research on the drought tolerance of seedlings or saplings remains limited (Van den Bilcke et al., 2013). Seed germination and seedling growth have been found to be enhanced in open canopy areas with higher light availability (Blumenfeld-Jones et al., 2006), a trait common among pioneer light-demanding fast-growing species. However, tamarinds have a slow growth rate (Sagar et al., 2021) and long lifespans (Winchester et al., 2018), challenging conventional expectations for pioneer species. The conventional understanding of forest succession, which classifies species as shade-intolerant pioneers or shade-tolerant old-growth species, is increasingly contested (Chazdon et al., 2010; Poorter et al., 2019). New frameworks such as the stature-recruitment axis have been proposed to better understand forest dynamics during succession (Rüger et al., 2020). In light of these theories, assessing tamarind's life history traits such as seed germination rates and seedling growth patterns is crucial for their effective management and use in restoration projects. Addressing the gaps in our understanding of their early-stage drought tolerance and life history of tamarinds is vital for the conservation of this important species.

Seed germination and seedling growth and survival are intricately influenced by resource availability (e.g., light, water, and nutrients) (Bhadouria et al., 2016). Both light quality and intensity play a pivotal role in seed germination, seedling establishment, and early growth (Gommers and Monte, 2018). Recent research has shown that water availability (rainfall and soil moisture) influences seedling growth not only in terms of the overall amount of water but also in the frequency of water supply (Li et al., 2022). Frequency is important because future climate scenarios predict variability in the seasonality and total amounts of rainfall (Pascale et al., 2016). Seedlings are particularly vulnerable to a limitation in resources like water and light because their low biomass can restrict resource capture both above- and belowground (Kupers et al., 2019). Thus, seedling and sapling stages are generally considered to be the most important bottleneck for successful plant regeneration (Poorter and Markesteijn, 2008).

The interplay between light and water limitations has long intrigued plant physiologists and ecologists, leading to debates about potential trade-offs between shade and drought tolerance (Holmgren et al., 2012; Gaviria and Engelbrecht, 2015). Central to these debates is the idea that plants experience a trade-off in their allocation to roots or leaves to maximize resource capture. The trade-off hypothesis (Smith and Huston, 1989) predicts that low water availability will have a stronger negative impact on plants growing in low light because plants might increase their light capture at the expense of water capture. The opposite is predicted by the facilitation hypothesis (Holmgren, 2000), where plants in low light (e.g., plants in shade in natural settings) have microclimatic conditions that mitigate the lack of water availability. In contrast, other studies argue that responses to these varying levels of resources are independent, because traits that confer drought resistance are uncoupled from those that maximize light capture (Sack and Grubb, 2002; Markesteijn and Poorter, 2009).

Functional traits constrain the mechanisms through which plants respond to deficits in resources like water or light (Poorter and Markesteijn, 2008) and can determine growth and establishment. At low light availability, morphological traits related to light capture such as a high specific leaf area (SLA) or allocation traits such as a lower root-to-shoot ratio can result in increased growth or survival (Liu et al., 2016). At low water availability, physiological and morphological traits such as lower stomatal conductance and lower stomatal density help avoid water loss via transpiration. Likewise, traits related to water capture such as a high root-to-shoot ratio can be advantageous for growth. However, the interplay between different resource levels complicates our understanding of these responses (Bhadouria et al., 2017). To advance our understanding and contribute to the effective establishment of tamarind in its natural habitat and to anticipate responses under future climate change scenarios, it is imperative to unravel the species' responses across varying levels of water and light availability (Sack and Grubb, 2002; Holmgren et al., 2012).

In this study, we focused on the critical early life-history stages for tamarind establishment and conducted three greenhouse experiments to investigate how the essential resources of light and water affect *Tamarindus indica* seed germination, seedling/sapling survival, growth, biomass partitioning, and physiology. We evaluated three questions: (1) What are the effects of light and water availability on seed germination, seedling survival, and growth? (2) What are the effects of different levels of water availability and watering frequency on tamarind sapling growth? (3) What are the morphological and physiological responses of tamarind seedlings and saplings to the different levels of light availability and watering availability/frequency? Our questions led to four predictions: (1) Tamarind seeds would exhibit lower germination under lower light and water availability. (2) Tamarind seedlings would exhibit lower survival and growth under low light and drier conditions. (3) Seedlings in low light would allocate more resources to leaves to maximize light capture, resulting in a lower root-to-shoot ratio. (4) Water availability and watering frequency would strongly influence tamarind sapling growth and physiology. Results from this study can inform restoration practices in areas where tamarinds are declining. Furthermore, this research contributes to a better understanding of plant responses to drought conditions, thereby improving predictions of plant responses to future climate change (Brodribb et al., 2020).

MATERIALS AND METHODS

To answer our questions, we set up three different and independent experiments in a controlled environment within a greenhouse facility at the University of Minnesota (Saint Paul, Minnesota, USA) using seeds that we extracted from tamarind fruits bought from a local provider, who imports produce from Mexico. Due to the constraints of the COVID-19 lockdowns, these were the only available seed sources in required quantities for the experiments. Temperatures in the greenhouse were set to an average of 21°C (at night) and a maximum of 26°C (at noon), and daylength was 12 h.

Experiment 1: Effect of light and water availability on seed germination

We sowed 300 seeds in Sungro Professional Growing Mix (Sun Gro Horticulture, Agawam, MA, USA), which contains a mix of bark, sphagnum peat moss, perlite, and dolomite lime in germination trays ~5 mm deep. The average seed mass was 1.05 g (range: 0.70–1.31 g). Seeds were placed in low light, medium light, or high light treatments. To impose the light treatments, we built three shade houses made of PVC pipes and shade cloths to simulate three forest light conditions. Photosynthetic active radiation (PAR) in the greenhouse was measured as photosynthetic photon flux (PPF; μmol m^{-2} s^{-1}). In the full light treatment, seeds were exposed to an average of 970 μmol m^{-2} s^{-1} at midday, representing open areas in the forest. The medium light treatment replicated light conditions in a small forest gap, with seeds receiving 10–15% of full light (average 120 μmol m^{-2} s^{-1} at midday). In the low light treatment, seeds were exposed to 1–2% of full light (average 9 μmol m^{-2} s^{-1} at midday). This treatment represented a closed canopy in a forested environment (Montgomery and Chazdon, 2001; Poorter and Markesteijn, 2008; Zhou et al., 2023). The chosen light values are representative of gallery forests in Madagascar, which have a denser canopy than the more open dry forests, and where tamarinds are dominant. We chose the dry forests of southern Madagascar as a reference, because in this region tamarinds are dominant but experiencing significant decline (Mondragón-Botero et al., 2024). Madagascar is one of the best documented locations for tamarind decline, with comprehensive studies available (Sussman and Rakotozafy, 1994; Blumenfeld-Jones et al., 2006; El-Siddig et al., 2006; Sagar et al., 2021), and we have substantial experience working in this region. In each light treatment, half of the seeds ($N = 100$) were watered manually three times per week to keep the soil moist, and the other half were not watered at all. Within each combination of water and light, half of the seeds were scarified before sowing by making 5–10 small cuts with a nail clipper to evaluate the effects of this pre-germination treatment on seed germination. Each seed was monitored for germination up to 30 days after sowing.

Experiment 2: Effect of light and water availability on seedling growth

In a second independent experiment, we grew 300 tamarind seedlings (defined as plants younger than 3 months that had not dropped their cotyledons) in a full factorial design, using four watering treatments and the three levels of light described for Experiment 1. Seeds used for this experiment had an average mass of 1.06 g (range: 0.74–1.54 g) and were sourced from the same provider as those used in the first experiment. Each light treatment consisted of 100 seedlings, 25 seedlings per watering × light treatment. Seedlings were individually potted in 1-gallon pots (13 × 13 × 25 cm) filled with a mixture of 40% black soil, 30% sand, and 30% composted pine bark, and fertilized with 23 g of Osmocote Plus, a slow-release fertilizer (15 N:9 P:11 K; ICL, tel Aviv, Israel). The watering treatments were based on reference rainfall patterns in the dry forests in southern Madagascar, where tamarinds are native. Madagascar was chosen as a reference for the reasons previously stated (Diallo et al., 2007; Jolly, 2012; Winchester et al., 2018; Rigden et al., 2024). The no-water treatment group was only watered twice at the onset of the experiment to allow seed germination with no subsequent watering. For the other treatment groups, the high watering treatment represented a mean monthly rainfall of

TABLE 1 Watering treatments based on seasonal rainfall variations for experiments 2 and 3.

Watering level	Monthly rainfall equivalent (mm)	Water volume per week (mL)	Water volume per watering event (mL)
No water	0	0	0
Low	50	210	70
Medium	200	845	281
High	400	1690	563

400 mm, which corresponds to an exceptionally wet month in the area. The medium watering treatment represented a mean average month during the rainy season averaging 200 mm of rain. The low watering treatment (50 mm) reflected the average rainfall during the drier months (Table 1). These watering treatments were applied from the time the seeds were sowed and continued throughout the experiment. The weekly volume of water for each treatment, as detailed in Table 1, was based on the pot surface area of 0.17 m^2 and was evenly distributed across three watering events per week to maintain consistent soil moisture levels. Soil moisture was monitored and measured as volumetric water content (% volume) using a soil moisture sensor (SM150 Soil Moisture Kit, Delta-T Devices, Cambridge, UK). We recorded seedling survival and stem diameter and height weekly over 4 months. At the end of the experiment, all seedlings were harvested and measured (see Functional traits and physiological variables).

Experiment 3: Effect of water availability and watering frequency on sapling growth

We then investigated the impact of water availability and watering frequency on the early growth and physiological performance of tamarind saplings. We define these plants as saplings because at the moment of harvesting they were 6 months old, had a woody stem, and had lost their cotyledons. For this experiment, we cultivated a total of 150 tamarind individuals using an independent batch of seeds in the greenhouse. These plants were grown in 1-gallon pots (13 × 13 × 25 cm) containing a substrate comprising 40% black soil, 30% sand, and 30% composted pine bark, and fertilized with 23 g of Osmocote Plus. Before the start of Experiment 3, all plants had received the same watering regime of three times per week for 3 months and grown in uniform conditions. Then 25 plants were assigned to each of the four watering treatments described for Experiment 2 (Table 1). We also examined the influence of watering frequency on sapling growth. For this, two additional groups of plants were assigned to the medium watering treatment of 845 mL per week, with different watering frequencies. Group 1 was watered once a week, while group 2 received water every 2 weeks. Thus, each individual received an equivalent amount of water, but the frequencies differed. The treatments were imposed for 3 months, after which all saplings were harvested and numerous variables measured (see Functional traits and physiological variables).

Biomass allocation

To determine the stem, root, and leaf mass fraction, we harvested all plants and separated the stems, leaves and roots, and each part was weighed fresh, then dried at 65°C for at least 3 days and weighed again. Mass fractions were calculated by dividing the dry mass of each component by the total aboveground biomass. The root-to-shoot ratio was calculated by dividing the dried root biomass by the dried aboveground biomass (i.e., stem plus leaves), and the ratio was expressed as a percentage.

Functional traits and physiological variables

Specific leaf area (SLA) and leaf dry matter content (LDMC) were measured using standard protocols (Pérez-Harguindeguy et al., 2013). We sampled five fully expanded leaves including their petioles from each individual plant. Fresh leaves were weighed, dried in an oven at 65°C for 72 h, and weighed again. Leaf area (LA) was determined by scanning each fresh leaf using an Epson scanner and processing the images in ImageJ software (Rasband, 2016). We calculated SLA ($cm^2\ g^{-1}$), by dividing the leaf area by the corresponding dry mass, and LDMC ($mg\ g^{-1}$), was obtained by dividing the dry mass of the leaves by their fresh mass. For stomatal density measurements, clear nail polish impressions were taken from the abaxial surface of selected leaves and observed with a light microscope to count the stomata to calculate stomatal density (number of stomata per square centimeter).

A random subgroup of plants in Experiment 2 and 3 were selected for physiological measurements. We measured the predawn maximum quantum efficiency of photosystem II (F_V/F_M). To ensure accurate measurements, we utilized dark adaptation clips to block all light and dark acclimate the seedlings overnight. F_V/F_M was calculated as the ratio of variable ($F_M - F_0$) to maximum fluorescence (F_M). Measurements were done with a OS30p+ Chlorophyll Fluorometer (Opti-Sciences, Hudson, NH, USA). Additionally, we measured stomatal conductance at midday (mol $H_2O\ m^{-2}\ s^{-1}$) using a handheld porometer (Decagon Devices, Pullman, WA, USA). Finally, midday leaf water potential (Ψ_L in MPa) was measured to assess water stress of the saplings in Experiment 3 just before harvest using a pressure chamber. All traits were measured at the end of the experiment before harvesting the plants to measure biomass allocation. Plants in the no-water treatment were excluded from these measurements because they had lost their leaves, and only plants that received water were measured.

Statistical analyses

We evaluated the effect of light and water availability and their interactions with scarification on seed germination using a generalized linear model (GLM) with a binomial distribution (Gianinetti, 2020). A type III ANOVA was used to test the effect of light and water availability on tamarind seedling growth, allocation, traits, and physiology, followed by a Games-Howell test if we found differences between treatments. Since seedlings and saplings were growing during the experiments, we performed linear regressions of shoot versus root biomass for each treatment group. This approach allowed us to visually compare the regression slopes across treatments and differentiate allometric effects from treatment effects (Poorter et al., 2012). All statistical analyses were conducted in R version 4.3.1 (R Core Team, 2023) using the packages Tidyverse (Wickham et al., 2019), emmeans (Lenth, 2023), car (Fox and Weisberg, 2019), userfriendlyscience (Petersen, 2020), and multcomp (Hothorn et al., 2008).

RESULTS

Experiment 1: Effect of light and water availability on seed germination

Seed germination did not differ among light levels. Contrary to our hypothesis, there was no evidence that germination in medium light levels ($z = -0.29$, $P = 0.77$) nor full light levels ($z = 0.29$, $P = 0.78$) differed from low light levels. Scarifying the seeds before sowing did not have a strong effect on seed germination ($z = 0.70$, $P = 0.48$). Furthermore, an analysis of scarification and its interaction with light did not provide strong evidence to suggest that the effect of scarification was modified by the light intensity. Scarifying the seeds before sowing slightly enhanced germination only at medium light levels from 64% to 96%. However, the overall effect was variable across light environments and not significant ($z = 1.16$, $P = 0.25$). Lastly, we found that watered seeds had a high germination percentage (84%), whereas none of the unwatered seeds germinated, indicating that water availability was the primary determining factor for seed germination (Figure 1).

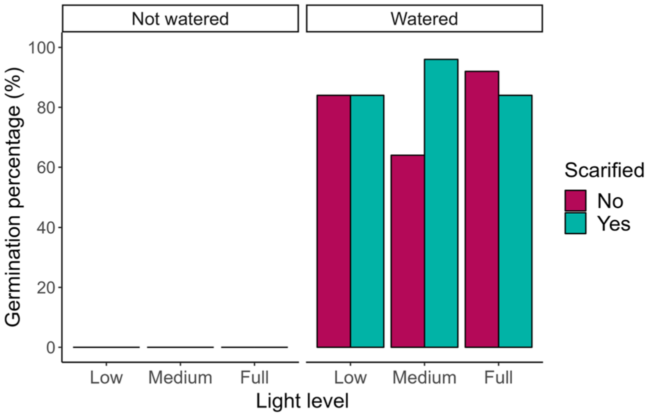

FIGURE 1 Tamarind seed germination percentages at 30 days post treatment among the different light and watering levels for scarified or intact tamarind seeds. Bars represent the total germination percentage for each treatment combination. Different colors in the bars represent the seeds that were or were not scarified before sowing. The statistical tests were conducted on the binomial responses of germination (germinated or not germinated) plots show germination percentages for clarity.

Experiment 2: Effect of light and water availability on seedling growth

Light availability strongly impacted tamarind seedling growth quantified in terms of height ($F = 8.83$, $P < 0.001$), stem diameter ($F = 25.47$, $P < 0.001$) and final biomass ($F = 3.44$, $P = 0.07$). Compared to seedlings in medium light, seedlings in low light were 26% shorter, had a 16% smaller stem diameter, and 65% less biomass. When compared to seedlings in high light, seedlings in low light were 39% shorter, had a 28% smaller stem diameter, and 77% less biomass (Figure 2; Appendix S1). In low light, the differences in plant height across water availability levels were minimal, which suggests that light is the limiting factor for growth rather than water. However, as light availability increased (medium and high light levels), response to light was modulated by water availability, and we found strong evidence for an interaction between both resources (height: $F = 3.40$, $P = 0.06$; stem diameter: $F = 3.43$, $P = 0.07$; biomass: $F = 3.13$, $P = 0.07$). As expected, plants that were not watered were shorter, had smaller stem diameters and less biomass, regardless of the light intensity. In the medium and full light treatments, tamarinds with higher water availability (medium and high watering treatments) were taller, with larger diameters, and more biomass. For example, fully watered tamarind seedlings under full light had on average 127% more biomass than those in medium light. None of the seedlings in the unwatered treatment survived to the end of the experiment. By contrast,

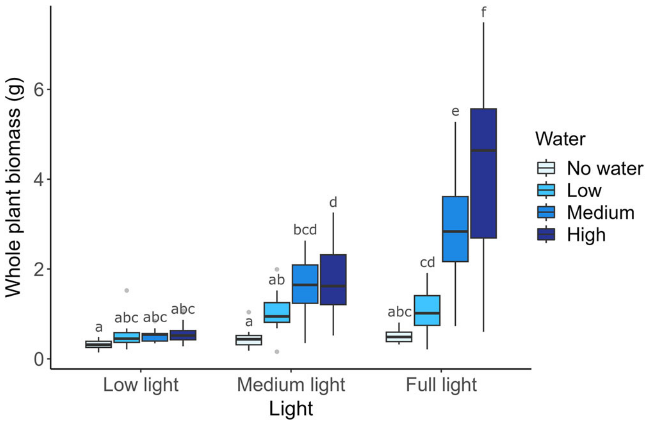

FIGURE 2 Tamarind seedling dry biomass in three light and four watering levels. Low light: 9 µmol m^{-2} s^{-1}, medium: 120 µmol m^{-2} s^{-1}; high: 970 µmol m^{-2} s^{-1} (all at midday). Low water: 210 mL, medium: 845 mL, high: 1690 mL. Different letters above the bars denote differences with strong statistical support (post hoc Games–Howell test, $P < 0.05$).

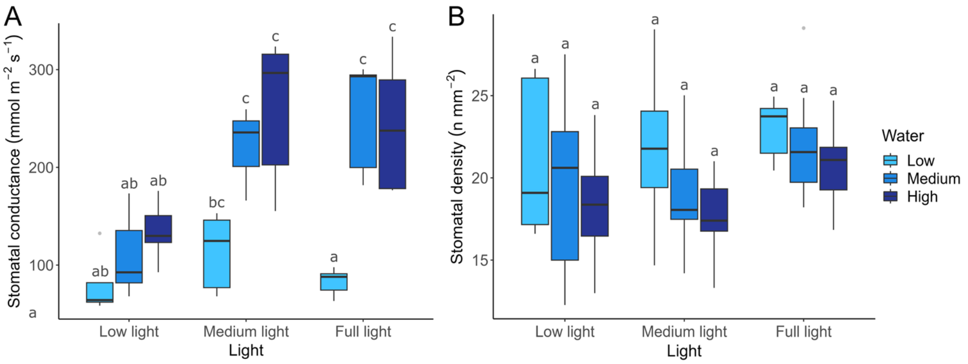

FIGURE 3 Tamarind seedling stomatal conductance (A) and stomatal density (B) under three light conditions and three watering levels. Low light: 9 μmol m^{-2} s^{-1}, medium: 120 μmol m^{-2} s^{-1}; high: 970 μmol m^{-2} s^{-1} (all at midday). Low water: 210 mL, medium: 845 mL, high: 1690 mL. Different letters above the bars denote differences with strong statistical support (post hoc Games–Howell test, $P < 0.05$).

seedlings in all other watering levels across the four light levels had high survival rates that ranged from 88% to 100% depending on the treatment combinations (Appendix S2).

As hypothesized, root-to-shoot ratio increased with an increase in light intensity ($F = 5.66$, $P = 0.004$). However, there was no evidence that the root-to-shoot ratio was affected by water availability ($F = 0.58$, $P = 0.56$), and there was no support to indicate an interaction between water and light ($F = 1.60$, $P = 0.18$) (Appendix S3). The regression lines for different light treatments diverged in slope, indicating that the observed variations in root-to-shoot ratios are attributable to the imposed light treatments rather than being solely a consequence of allometric growth (Appendix S4). A detailed analysis of biomass fractions with increasing light levels showed that the difference in root-to-shoot ratio was mostly driven by an increase in leaf biomass and a decrease in root biomass while stem biomass remained constant (Appendix S2).

The tamarinds had nuanced morphological and physiological responses to water and light availability and their interplay, and patterns differed for morphological and physiological traits. Specific leaf area differed strongly among light treatments ($F = 416.36$, $P < 0.001$); mean SLA was 63% higher in low light (mean 35.66 mm^2 mg^{-1}) compared to high light (21.81 mm^2 mg^{-1}). Specific leaf area differed slightly among water levels ($F = 2.96$, $P = 0.025$), and there was strong evidence for an interaction between water and light on SLA ($F = 5.07$, $P = 0.002$). Higher water levels significantly increased SLA in low light, but this effect diminished with more light exposure (Appendix S5A). Similarly, LDMC differed among light ($F = 40.30$, $P < 0.001$) and water levels ($F = 267.61$, $P < 0.001$). There was a 26% increase in LDMC for seedlings in high light (282.43 g mg^{-1}) compared to those in low light (207.85 g mg^{-1}) (Appendix S5B).

Stomatal conductance, by contrast, increased with increasing water availability but this effect varied across the different light levels ($F = 2.64$, $P = 0.05$). Plants subjected to low water availability consistently had low stomatal conductance, irrespective of light levels (Figure 3A). Finally, chlorophyll fluorescence remained consistent across varying light and water levels (water: $F = 0.27$, $P = 0.77$; light: $F = 1.03$, $P = 0.37$). Similarly, our data showed that neither light nor water had an effect on stomatal density (light: $F = 0.63$, $P = 0.54$; water: $F = 0.93$, $P = 0.39$) (Figure 3B).

Experiment 3: Effect of water availability and watering frequency on sapling growth

There was a significant effect of water amount on sapling height and diameter, but no effect of watering frequency. Tamarind saplings subjected tono or low water conditions were 42 to 22% shorter ($F = 38.05$, $P < 0.001$) and had smaller stem diameters ($F = 25.17$, $P < 0.001$), and 70 to 41% less total dry biomass ($F = 33.70$, $P < 0.001$) than those with medium or high watering (Figure 4A, Appendix 6). Post hoc analysis showed that plant height, stem diameter, and total dry biomass did not differ among medium and high water levels. Similarly, watering treatments influenced the root-to-shoot ratio. The root-to-shoot ratio decreased as the watering amount increased ($F = 17.13$, $P < 0.001$), signifying a transition toward prioritizing aboveground growth in well-hydrated conditions (Figure 5). However, this trend was observed in the zero to medium water, but not in the medium to high water levels. The observed root-to-shoot ratio pattern was driven mainly by the opposite responses in leaf and root biomass fractions among treatments. Root biomass fraction decreased as the watering level increased ($F = 17.96$, $P < 0.001$), whereas leaf biomass fraction increased ($F = 12.67$, $P < 0.001$). On the contrary, the stem biomass fraction did not change with the watering treatment ($F = 2.56$, $P = 0.059$). The slopes of the regression lines for each watering frequency differed, indicating that the specific watering protocols did have an effect on the root-to-shoot ratio and that this effect was not only due to allometric scaling of the saplings. Slopes for the high-watering treatments were notably steeper (indicating greater allocation to shoot biomass), contrasting with the more gradual slopes observed in lower-watering treatments (Appendices 4 and 6).

Watering frequency did not affect sapling growth. Height ($F = 0.37$, $P = 0.69$), stem diameter ($F = 0.88$, $P = 0.42$), and dry biomass ($F = 2.23$, $P = 0.12$) did not differ among the three different water frequencies (Figure 4B; Appendix 6). Likewise,

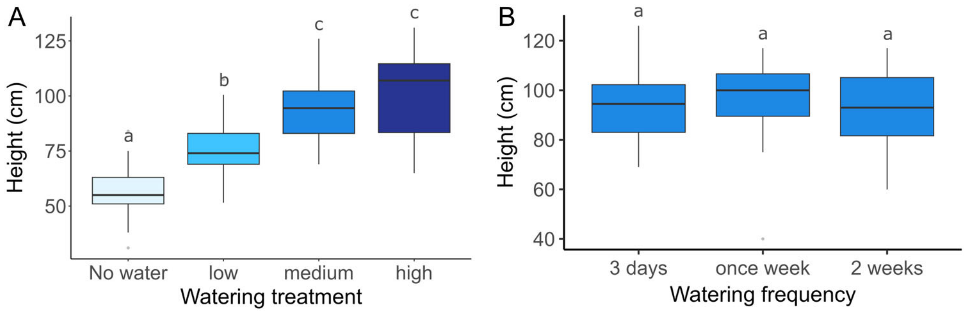

FIGURE 4 Tamarind sapling height within (A) each watering treatment (total weekly volume: low, 210 mL, medium: 845 mL; high, 1690 mL) and (B) for the different watering frequencies (845 mL every 3 days). Different letters above the bars denote differences with strong statistical support (post hoc Games–Howell test, $P < 0.05$).

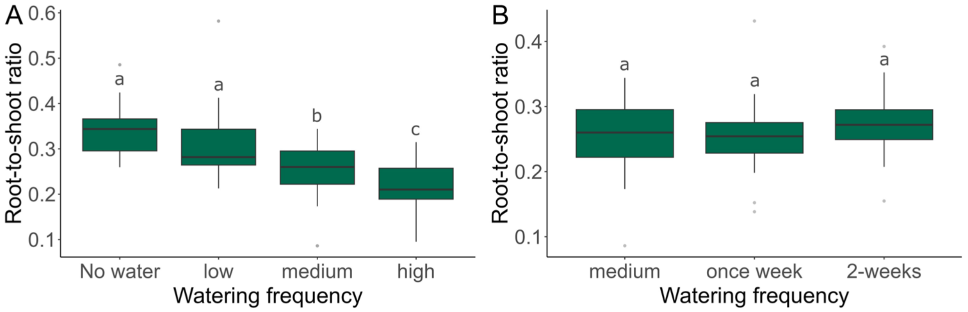

FIGURE 5 Tamarind sapling root-to-shoot ratio within (A) each watering treatment,(total weekly volume: low, 210 mL, medium: 845 mL; high, 1690 mL) and (B) for different watering frequencies. Different letters above the bars denote differences with strong statistical support (post hoc Games–Howell test, $P < 0.05$).

the root-to-shoot ratio was similar among the three watering frequencies ($F = 1.44$, $P = 0.25$) (Figure 5).

In the saplings, water availability affected SLA ($F = 4.86$, $P = 0.017$) but not LDMC ($F = 2.85$, $P = 0.08$). Specific leaf area was highest for the low water availability (21.41 $\text{mm}^2\ \text{mg}^{-1}$) compared to medium (18.05 $\text{mm}^2\text{mg}^{-1}$) and low watering levels (17.74 $\text{mm}^2\ \text{mg}^{-1}$). Watering frequency did not have an effect on SLA ($F = 3.08$, $P = 0.07$) or LDMC ($F = 1.73$, $P = 0.19$) (Appendix 7). Stomatal conductance differed across watering levels ($F = 13.22$, $P = 0.001$) but not among watering frequencies ($F = 0.14$, $P = 0.87$). Mean stomatal conductance for the low water treatment was 31.25 mmol $\text{m}^2\ \text{s}^{-1}$, increasing to 134.44 mmol $\text{m}^2\ \text{s}^{-1}$ for the medium watering level and 171.71 mmol $\text{m}^2\ \text{s}^{-1}$ for the high watering level. Chlorophyll fluorescence did not differ across watering levels ($F = 0.42$, $P = 0.66$) or watering frequencies ($F = 0.23$, $P = 0.79$). Last, midday water potential was substantially lower in the low watering treatment, dropping to as low as −3.04 Mpa. In contrast, the high watering treatment maintained a higher average water potential of −1.08 MPa. However, water potential did not differ among watering frequencies ($F = 0.22$, $P = 0.80$) (Appendix 8).

DISCUSSION

Tamarinds play a crucial role in sustaining rural communities of local people and are an important food species for wild animals in dry forests, making their decline a cause for concern. We focused on understanding the resource requirements during the critical early phases of seedling establishment and demonstrated that tamarind seed germination is affected by water but not by light or scarification as a pre-germination treatment. We suggest that seed germination is not likely the bottleneck stage in tamarind reproduction within forest ecosystems. Instead, the focus should extend to subsequent stages, such as seedling establishment and growth. Our findings highlight the nuanced relationship between light and water availability on tamarind seedling and sapling growth, emphasizing the importance of considering both factors in tamarind restoration projects. We also found that watering frequency had no effect on tamarind growth or physiology, suggesting that tamarinds might not be as sensitive to changes in rainfall periodicity but to changes in the total amount of precipitation. Although the reasons for its decline in its native range remain unknown, our study provides valuable insights for guiding tamarind restoration efforts in the field.

Tamarind seed germination

Water emerged as the primary factor determining seed germination, aligning with the widely acknowledged significance of water as the most important external factor for seed germination (Koller and Hadas, 1982). In natural settings, this finding could translate into tamarind seeds germinating easily in response to water cues (i.e., rainfall). Indeed, research conducted in the Berenty Reserve in Madagascar showed that the forest floor was covered with tamarind seedlings after the rains and that seeds germinated equally well after dispersal through endozoochory by lemurs (Mertl-Millhollen et al., 2011). We obtained a high germination percentage of commercially available seeds in our study. Similarly, other experiments have obtained germination percentages ranging from 50 to 100% (Muhammad and Amusa, 2003; Fandohan et al., 2011). This convergence of field evidence and experimental results does not support the hypothesis of poor seed germination as a hindrance to tamarind recruitment in the forest (Muhammad and Amusa, 2003).

Both light quality and quantity have been demonstrated to be crucial for promoting or inhibiting seed germination in various species (Kyereh et al., 1999; Vargas-Figueroa, 2015; Carvalho et al., 2021). Our study is one of the first to test the effects of light in tamarind seed germination. Our results indicated high germination irrespective of light levels, suggesting an adaptability to varying light conditions which implies that tamarind seeds can successfully germinate in closed canopy areas in the forest, or in very open forest areas which might confer an advantage for dispersal and colonization.

Contrary to several studies that have highlighted the benefits of scarification and other pre-germination treatments in improving germination percentages (Fandohan et al., 2011; Oliveira et al., 2017; Segato et al., 2017; Garba et al., 2020) our research found that these methods did not significantly enhance the germination of tamarind seeds. Our findings suggest that such pre-treatments may not be essential for achieving high germination rates in tamarind. However, scarification may speed up germination (El-Siddig et al., 2006; Fandohan et al., 2011), which could offer practical advantages in a nursery setting, where the speed of germination is a valuable factor for tamarind seedling production.

Do tamarinds support a trade-off in response to light and water availability?

Our results offer nuanced support for the trade-off hypothesis. Tamarind growth was influenced by the interaction between light and water availability, with the negative impact of low light levels on growth being more pronounced under conditions of low water availability. This interaction is in line with the trade-off hypothesis that assumes that a plant has constraints to tolerate low levels of a resource when another resource is limiting as well. The lack of increased growth with additional water in low light suggests that when light is the limiting factor, the availability of water beyond a certain threshold does not contribute to further growth, which aligns with the hypothesis that a plant's growth is constrained under the simultaneous limitation of multiple resources (Smith and Huston, 1989; Holmgren, 2000).

As hypothesized, seedlings in low light allocated more resources to leaves to maximize light capture, resulting in a lower root-to-shoot ratio and higher specific leaf area. However, the lack of interaction between water and light availability in biomass allocation introduces a level of complexity into our interpretation. While the trade-off hypothesis holds true for growth, the underlying mechanisms could go beyond differential biomass allocation as suggested by the trade-off hypothesis. The observed patterns of resource allocation could be influenced by other physiological adaptations such as water-use efficiency or photosynthetic rates, which do not require big shifts in biomass allocation between roots and shoots (Sack, 2004; Kupers et al., 2019). In fact, tamarind seedlings have leaf and stem trichomes and finer root systems in water-limited conditions, enhancing soil water access and uptake (Van den Bilcke et al., 2013). Our results also indicate that responses in biomass allocation are influenced by light availability and that, for tamarinds, light dictates morphological responses more so than water as found for other species (Valladares and Niinemets, 2008).

Our findings contribute to the growing body of evidence that suggests that light/water trade-offs are not universally applicable across all growth and morphological traits (Kupers et al., 2019). Indeed, our results are consistent with a recent meta-analysis that found that drought and shade had positive interactive effects on photosynthesis and biomass production, meaning that shade alleviated drought stress effects, but they had orthogonal (unrelated) impacts on biomass allocation and leaf morphology (Wang and Wang, 2023).

Overall, our results indicate that tamarinds exhibit morphological and physiological plasticity. This adaptability of tamarind seedlings to diverse environmental conditions may explain the global distribution of tamarinds across a variety of climates (Bowe and Haq, 2010). Our findings align with other studies showing a decrease in stomatal conductance with declining soil water availability (Yin et al., 2016). While stomatal density and conductance are generally positively correlated (Aragón et al., 2023), we observed an uncoupled relationship between stomatal density and conductance. It may be that stomatal conductance adjustments in response to reduced water availability occur more through reductions in stomatal size rather than stomatal density (Doheny-Adams et al., 2012).

Although we observed low mortality, growth was reduced in low light and low water levels. Notably, our observation period was limited to several months, and the growth disadvantage observed could have implications for the subsequent survival of seedlings. We emphasize that our experiment took place in a controlled environment without exposure to temperature variations, pests, or herbivore pressure, factors that could significantly impact tamarind growth in natural settings. Consequently, high survival rates in our controlled conditions might not accurately reflect seedling survival rates in the wild. Follow-up studies monitoring tamarind growth in natural settings are needed to gain insights into the potential causes of the observed lack of recruitment.

Tamarind saplings responses to water availability and watering frequency

In our study, tamarind trees were subjected to a substantial variation in watering frequency that ranged from every 3 days to every 2 weeks. This regime represents a significant gradient in water frequency, especially given the constrained conditions of pot cultivation. However, despite this variation, watering frequency did not affect tamarind growth or biomass allocation. In contrast, other studies have shown that watering frequency affects growth and performance of tropical tree seedlings and saplings (Spence et al., 2016; Westerband et al., 2019; Li et al., 2022). As a consequence, these species might be vulnerable to future climate change scenarios characterized by altered rainfall patterns (Allen et al., 2017). Our findings suggest a certain resilience in tamarind, indicating a potential reduced sensitivity to changes in rainfall frequency but suggest that tamarinds will still be affected by a reduction in overall rainfall amounts. However, it is important to note that our conclusions apply to the range of watering frequency we examined, which included intervals up to 2 weeks. Longer intervals of drought were not studied, and thus, their impact remains uncertain.

Water availability had an effect on the root-to-shoot ratio during the sapling stage, contrary to its effect on seedlings, suggesting that tamarind's water requirements increase from the seedling to the sapling stage. Similarly, plant responses to drought and light availability can differ among life stages (Gaviria and Engelbrecht, 2015). Additionally, tamarind has large persistent and photosynthetic cotyledons during the seedling stage, which may partially compensate for the effects of limited water availability. In fact, the critical role of tamarind cotyledons was demonstrated in an experiment that showed significant reduction in seedling survival upon cotyledon removal (Oliveira and Morais, 1999).

An interesting finding was the absence of significant differences in plant biomass, SLA, and LDMC between the medium and high water treatments. Regardless of increased water availability, tamarind plants reach a growth plateau, which suggests that there is a threshold water requirement which was met in our medium water treatment. Tamarind saplings, adapted to thrive in arid environments, might efficiently use lower quantities of water, resulting in similar morphological and physiological responses under medium and high water treatments.

Responses to water stress

Anisohydric plants allow their water potential to become more negative under drought conditions and maintain physiological functions despite significant water stress, whereas isohydric plants maintain a relatively stable water potential by closing their stomata early during drought conditions (Martínez-Vilalta and Garcia-Forner, 2017; Lambers and Oliveira, 2019). Our study suggests that tamarind seedlings and saplings exhibit characteristics indicative of anisohydric behavior, due to the low water potentials they can reach under conditions of low water availability.

Our results also showed that under low water conditions with an average leaf water potential of –2 MPa, tamarinds can maintain an average stomatal conductance of 60 mmol m^{-2} s^{-1}, which is relatively high for water-stressed plants (Engelbrecht et al., 2002). Other studies on stomatal conductance of tropical seedlings have reported values of 300–400 mmol m^{-2} s^{-1} for well-watered seedlings and 10–30 mmol m^{-2} s^{-1} for water-stressed seedlings (Veenendaal et al., 1996; Engelbrecht et al., 2002; Amissah et al., 2015).

Our findings align with those of Van den Bilcke et al. (2013), who categorized tamarinds as exhibiting risk-taking behavior, characterized by negative water potentials resulting from water expenditure or attempts to extract water from the soil. In dry environments, however, sustained risk-taking behavior under prolonged low water availability may lead to whole-plant hydraulic failure, potentially resulting in severe consequences or mortality during long dry periods. Thus, this risk-taking behavior could explain tamarind mortality and lack of recruitment during long dry periods in its native range.

On tamarind life history

In the historical context of plant ecology, species have traditionally been classified along a slow-fast life history continuum, defined by a trade-off between growth and survival (Salguero-Gómez et al., 2016). On this continuum, fast-growing, light-demanding species with short lifespans have been typically designated as pioneers during ecological succession (Finegan, 1996). However, this notion is changing (Chazdon et al., 2010; Lai et al., 2021), and an orthogonal axis of variation, the stature–recruitment axis, has been proposed. This axis ranges from long-lived pioneer species (light demanding and fast growing with long lifespans and low recruitment rates) to short-lived-breeders (species that grow and survive poorly, remain short-statured, but produce many offspring) at the other extreme (Rüger et al., 2018, 2020). Adding to this complexity, recent studies indicate that many pioneer species in the dry forest have higher wood density (Chave et al., 2006), associated with slower growth rates, compared to those in the wet forests (Poorter et al., 2019, 2021). Where does tamarind fall along these axes? Tamarind trees challenge traditional ecological classifications. While they require light similar to pioneer species, their slow growth rate and high wood density (0.75–1.5 g cm^{-3}) (Van den Bilcke et al., 2013; Sagar et al., 2021) deviate from the expected traits of such species, but align with pioneer species traits in the dry forest. Moreover, tamarinds have a combination of long lifespans, with some individuals living over 400 years (Winchester et al., 2018), and low recruitment rates, partially consistent with one extreme of the stature–recruitment axis. This combination of traits suggests that tamarind may not fit neatly into existing categories occupying an intermediate stage combining attributes of the two orthogonal axes, defined as a light-demanding, slow-growing, long-lived tree with low recruitment rates.

Genetic variations and study limitations

We used commercially sourced seeds for our study, which were the only seeds available to us at the time. Understanding genetic differences is essential for the effective restoration and conservation of tamarinds. A study by Nyadoi et al. (2010) revealed that although there is a widespread global tamarind haplotype, there are also distinct haplotypes restricted to specific geographical regions (e.g., Kenya, Tanzania, and Mexico). Other studies have found that tamarind exhibits substantial genetic variability across its distribution from Africa to Asia and the Americas, affecting traits such as growth rates, reproductive traits, and fruit characteristics (Diallo et al., 2007; Rajamanickam et al., 2023; Kanupriya et al., 2024a, b). Studies have shown that genetic diversity is mostly concentrated within individual trees rather than between populations, suggesting a strong potential for local adaptation (Kanupriya et al., 2024a).

Commercially sourced seeds, like those used in our study from Mexico, often undergo selection for traits favorable in agriculture such as uniformity and quick germination (Tapia-Pastrana et al., 2012). However, considering that tamarind has not undergone extensive agricultural selection programs (Nyadoi et al., 2014; Rajamanickam et al., 2023), the reductions in or changes to genetic variability that accompany domestication might be less pronounced than for other crops. Nonetheless, we acknowledge that traits selected for commercial seeds may not accurately reflect the natural genetic diversity or ecological adaptability of wild populations. Consequently, using such seeds could lead to overestimations of germination success and growth potential in restoration projects.

Because we used commercial seeds, applying our results to restoration projects in native settings such as Madagascar should be done with caution. Future research should focus on comparative analyses of wild and cultivated tamarind populations across different environmental conditions. This approach will help guide effective conservation strategies that preserve its genetic diversity, ensuring its survival and adaptability. Additionally, understanding the genetic structure, as indicated by shared haplotypes among populations, can inform the selection of seed sources that best reflect the genetic landscape of targeted restoration areas.

The future of tamarind populations: implications for restoration

The question of why tamarinds are not recruiting remains elusive, with much of the existing research focused on early life history stages. Crucial information on seed dispersal and pollination is lacking (Mertl-Millhollen et al., 2011; Fandohan et al., 2012). Lack of seed pollinators can cause lower fruit yields (Diallo et al., 2008), and effective seed dispersal is crucial for reaching suitable conditions in the forest for tamarind establishment, including adequate light and water availability as shown in our study. In addition, more than 40 species of insects and various species of nematodes, natural pests, and pathogens have been shown to affect tamarind seed viability and plant health (Joshi and David, 2018; Kumar Gupta, 2018) possibly resulting in lower recruitment. Future research should address all these important topics to elucidate the reasons for tamarind decline in its natural habitat.

In the meantime, initiating tamarind restoration programs is necessary to ensure the long-term viability of this species in its native range. An initial important step for restoration is to understand the requirements for seed germination (Dalziell et al., 2022). Results from our study can be used to inform best practices for tamarind seed propagation in restoration initiatives. Our results underscore the important role of water in facilitating germination and the wide-ranging adaptability of tamarind seeds to diverse light conditions and also highlight that pretreatment scarification is likely not a necessary step to ensure high germination percentages. Finally, because light is not a limiting factor for the germination of tamarind seeds, trays or beds can be placed in a variety of locations within the nursery without the concern of light intensity inhibiting germination. This flexibility can be particularly useful in nurseries with space constraints or those that manage multiple species with different light requirements.

While tamarind seed germination does not depend on light, the growth and establishment of seedlings and saplings are impacted by light. Therefore, ensuring sufficient light availability in high light environments is crucial for the species optimal growth. Additionally, considering the risk-taking behavior of tamarinds during low water availability, we recommend watering tamarinds during the seedling and sapling stage. This practice is especially important when tamarinds are planted in the field to reduce mortality during the dry season. The ecological strategy of tamarind has significant implications for its management during restoration. For example, tamarind can be planted in areas with full sunlight. Yet, it grows slowly and thus might need to be managed for longer periods. Also, due to its low recruitment rates but long lifespans, it is crucial to enhance its recruitment in restoration sites. Given the many studies alerting about tamarind decline in the wild, we encourage more long-term studies on tamarind populations in its native range. Because mature trees are long-lived, there could be a long lag time between a strong reduction in recruitment of juveniles and its perception as a problem (Diallo et al., 2008), and tamarind recruitment could be halted in other areas of the world going but not noticed.

The implications of our findings extend beyond the specific ecology of tamarinds, offering insights into new ways of seeing succession dynamics. It also highlights the importance of light and water as key factors in ecological processes and how species can be influenced by the availability these two resources. Our study elucidates how these essential resources interact to shape plant performance and survival, highlighting their critical roles in the ecological trade-offs necessary for effective forest restoration. By integrating our understanding of these fundamental environmental factors, we can refine restoration strategies to better support the recovery and functionality of diverse forest ecosystems, ultimately fostering resilience and biodiversity in restored landscapes.

AUTHOR CONTRIBUTIONS

A.M.B. conceptualized the study, collected and analyzed the data, and wrote the initial draft of the manuscript. J.S.P. conceptualized the study, oversaw data collection and analysis, and contributed to manuscript preparation.

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DATA AVAILABILITY STATEMENT

All the data collected in this research can be found in Dryad: https://doi.org/10.5061/dryad.xwdbrv1q8.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Tamarind seedling height (A) and diameter (B) under three light conditions and four watering levels.

Appendix S2. Tamarind seedling survival for the different water and light treatments.

Appendix S3. (A) Tamarind seedling root-to-shoot ratio by light and watering treatments showing that RSR increased with increasing light but not watering. (B) Leaf, stem, and root biomass fractions showing that the increase in root-to-shoot ratio was due to an increase in root biomass and a decrease in leaf biomass; stem biomass remained constant.

Appendix S4. Relationship between shoot and root dry biomass for tamarind seedlings and saplings across varying watering and light treatments indicating treatment-induced shifts in biomass allocation.

Appndix S5. Tamarind seedling (A) specific leaf area and (B) leaf dry matter content under three light conditions and four watering levels.

Appendix S6. Comparative analysis of dry biomass, stem diameter, and biomass fractionation in tamarind saplings subjected to different irrigation treatments.

Appendix S7. Tamarind sapling specific leaf area for different watering (A) levels and (B) frequencies. Leaf dry matter content for different watering (C) levels and (D) frequencies.

Appendix S8. Physiological responses of tamarind saplings under different watering treatments.

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