

ORIGINAL ARTICLE

Vertical root development of seedlings grown in deep containers: Comparison of five tropical dry forest species in Myanmar

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ABSTRACT Deep-container seedlings (DCSs), which are grown in deep containers, are expected to promote reforestation in drylands. To examine the suitability for DCS cultivation in terms of vertical root development, we grew seedlings of five tropical dry forest species common in Myanmar (*Azadirachta indica*, *Tamarindus indica*, *Hesperethusa crenulata*, *Tectona hamiltoniana*, and *Eucalyptus camaldulensis*) in deep multi-stage adjustable rolled (M-StAR) containers (8-cm diameter, 60-cm depth). The M-StAR container is a new type of cylindrical polyethylene container with a ribbed sidewall. While these five species showed different leaf phenology and rooting strategies, all five species developed roots reaching the bottom of the containers and showed Dickson Quality Index values >2.4 at the end of the cultivation period. In all species, total and specific root lengths reflecting the root density increased with container depth, with the deepest section (50–60 cm) mainly filled with fine roots ($\phi < 1$ mm), suggesting that tropical dry forest species adopt the common adaptive strategy to exploit water in the deep layer. Seedlings of the five tropical dry forest species with different leaf phenology and rooting strategies grew successfully in M-StAR containers. These results suggest that the DCS technique could also be applied for reforestation with other tropical dry forest species.

Key words: deep-container seedling, vertical root development, tropical dry forest species, M-StAR container, specific root length

INTRODUCTION

Dry forests characterized by several-month-long dry seasons occupy approximately half of the tropical and subtropical forest areas globally (FAO 2012, Siyum 2020). They are characterized by high species diversity, with many endemic and economically valuable species (Sánchez-Azofeifa et al. 2005), and provide a wide range of ecosystem services that sustain the livelihoods of local people. Despite their importance, dry forests have been constantly at risk of degradation, and planting seedlings of indigenous and/or introduced tree species, including enrichment planting, has long been a practical and effective activity to restore degraded dry forests (Griscom and Ashton 2011).

One of the technical constraints encountered in dryland reforestation is the existence of a distinct drought period,

which causes high seedling mortality at the early stages after outplanting (Padilla and Pugnaire 2007). Seedling mortality in drylands at this stage is mainly caused by low water availability to the roots, of which the distribution is limited to the dry upper soil layers (Gilbert et al. 2001). Several studies have shown a positive relationship between rooting depth and plant survival in drylands (Ovalle et al. 2015; Padilla et al. 2007). Therefore, it is important to raise seedlings with optimal morpho-physiological traits in the nursery phase, which facilitate rapid vertical root development immediately after outplanting (Cortina et al. 2013; Grossnickle 2012; Tsakalimi et al. 2005). Size, shape, and structure of the seedling container strongly influence the root morphological traits (Landis and Nisley 1990); thus, many studies have focused on determining the appropriate container design (Dominguez-Lerena et al. 2006; Mariotti



et al. 2015b; Pinto et al. 2011).

Deep-container seedlings (DCSs), as the name suggests, are grown in deep containers to maximize the deep-rooting potential of dry forest tree species and are expected to promote reforestation in drylands. The performances of DCSs grown in deep containers with depths >30 cm have been tested for Mediterranean species, such as *Quercus* spp. (Chirino et al. 2008; Mariotti et al. 2015a, b; Pemán et al. 2006), *Juniperus* spp. (Gülcü et al. 2010), and *Acacia* (= *Vachellia*) *caven* (De La Fuente et al. 2017), as well as riparian species (Dreesen and Fenchel 2010; Sagrera et al. 2013). Previous studies on DCSs indicated that the roots of DCSs can penetrate into deeper substrate layers than normal-depth container seedlings, when transplanted to larger container and grown during a certain period under optimum growing conditions (Chirino et al. 2008; De La Fuente et al. 2017). Sagrera et al. (2013) also concluded that the improved growth of DCSs was related to the improved access of the roots to deep water layers.

To take full advantage of DCS in terms of the deep soil layer accessibility after outplanting, the seedling roots should reach the bottom of the growth container during the nursery phase. However, as the magnitude of the rooting response to deep containers varies among species (Mariotti et al. 2015a, b), not all species may develop roots to the bottom of deep containers within the cultivation period.

Container costs for DCSs should also be considered for practical application. From the viewpoint of cost effectiveness, a multi-stage adjustable rolled (M-StAR) container invented by Mitsugi (2010) is expected to be widely accepted as an innovative tool for DCS cultivation in drylands (approximately 0.9 USD/M-StAR container in Japan as of September 2017). M-StAR is a cell container molded by rolling up a black polyethylene logistics sheet named APTON® (Shikoku Kakoh Co., Ltd., Kagawa, Japan). Although the depth of M-StAR containers originally used in humid temperate forests in Japan is approximately 15 cm, both the depth and diameter of M-StAR containers can be flexibly adjusted according to the planting purpose and target species. The openability of the sidewall is another advantage of M-StAR containers that facilitates easy removal of root balls from the containers. Additional advantages of M-StAR containers are that they are light (<100 g/container), recyclable, and highly durable.

In the current study, we selected five common tropical dry forest species in Myanmar considering the variation of leaf phenology and root morphological traits and raised DCSs of these species in M-StAR containers. According to the growth and root development analyses of these DCSs, we examined the suitability of these species for DCS cultivation. We especially focused on the root biomass, root

length, and specific root length (SRL) as the species-specific characteristics in vertical root development.

MATERIALS AND METHODS

Tree species

The following five woody species were selected for the study: *Azadirachta indica* A. Juss, *Tamarindus indica* L., *Hesperethusa crenulata* (Roxb.) M. Roem, *Tectona hamiltoniana* (Wall.) Kuntze., and *Eucalyptus camaldulensis* Dehnh. These species are commonly planted for community-based reforestation in the central dry zone of Myanmar. *A. indica* and *T. indica* are localized species, whereas *H. crenulata* and *T. hamiltoniana* are indigenous and deciduous species in Myanmar. *E. camaldulensis* was introduced to Myanmar from Australia. The selected species represent different leaf phenology and root characteristics (Table 1).

Design of M-StAR containers

M-StAR containers for DCS cultivation were formed by rolling up an APTON®, which is a single-face corrugated polyethylene sheet, into a bottomless cylinder to allow air pruning, and has a ribbed inner wall structure to assist vertical root development without spiraling (Fig. 1). The container depth was fixed at 60 cm to ensure both sufficient depth and convenience of the operation. The diameter was fixed at 8 cm to ensure both convenience of operation and optimal seedling growth based on suggestions in previous reports on the effect of small container diameters on seedling growth (Dominguez-Lerena et al. 2006). The bottom was covered by a polyethylene net with a 5-mm mesh to avoid substrate loss during the cultivation period. The container sheet was bound using zip ties at three depths to fix the shape during the cultivation period. DCSs were placed above ground level for air pruning with the support of a wooden rack at a growing density of 60 seedlings/m².

Preparation of DCSs

Preparation of DCSs consisted of the processes, that is, seeding in the seedbed, germination there, transplantation into M-StAR containers, and cultivation in the containers. All these processes were conducted in an open-air nursery at the Forest Department in Nyaung-U Township, Mandalay Division, Myanmar (21° 8' 41.7-N, 94° 56' 24.4-E).

Table 1. Species characteristics, initial size at transplantation, and sampling times (days after transplantation). The size at transplantation from seedbeds to M-StAR containers is presented as the mean $\pm$ standard error ($n = 5$).

Species	Origin	Family	Leaf phenology ^a	Root characteristics ^b	Size at transplantation		Sampling times (days after transplantation)			
					Seedling height (cm)	Total root length (cm)	1 st	2 nd	3 rd	4 th
<i>Azadirachta indica</i>	Localized species	Meliaceae	Evergreen	Deep taproot	8.22 $\pm$ 0.57	7.34 $\pm$ 0.39	1 (Nov 2017)	75	155	215
<i>Tamarindus indica</i>	Localized species	Caesalpinioideae	Evergreen	Deep taproot	2.35 $\pm$ 0.43	8.17 $\pm$ 0.75	1 (Jan 2018)	40	120	180
<i>Hesperethusa crenulata</i>	Indigenous local species	Rutaceae	Deciduous	Not reported	2.21 $\pm$ 0.15	6.64 $\pm$ 0.57	1 (Nov 2017)	75	155	215
<i>Tectona hamiltoniana</i>	Indigenous local species	Verbenaceae	Deciduous	Not reported	2.81 $\pm$ 0.17	4.38 $\pm$ 0.18	1 (Dec 2017)	60	140	200
<i>Eucalyptus camaldulensis</i>	Introduced species	Myrtaceae	Evergreen	Deep taproot	4.27 $\pm$ 0.26	4.58 $\pm$ 0.36	1 (Dec 2017)	60	140	200

^a Source: FAO 1986; Thein and Ba 2005

^b Source: Jobbágy and Jackson 2004; El-Siddig et al., 2006; Das and Chaturvedi, 2008

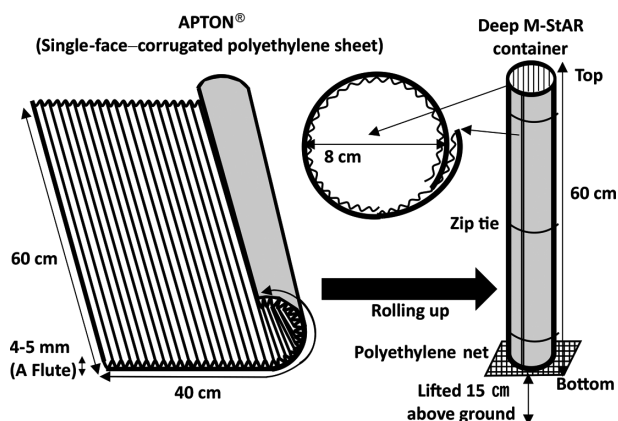


Fig. 1. Structure of the APTON® sheet and M-StAR container used for deep-container seedlings in the current study.

Seeds of the five tested species were collected locally and sown in sand seedbeds. Germinated seedlings were raised until the appearance of a true leaf (after approximately 1 month) and were then transplanted to M-StAR containers. The transplantation times differed among species (Table 1), as the seeds were sown immediately after collection from the mother trees owing to the lack of storage facilities.

The cultivation of DCSs in the M-StAR containers spanned from November 2017 to July 2018, covering different time periods depending on the transplanted time. The M-StAR containers were filled (at 2–60-cm depth) with coconut peat (coir dust), which had been rinsed with river water with electric conductivity $< 50 \text{ mS m}^{-1}$ and then air-dried. The filling (bulk) density of the substrate

was $0.07\text{--}0.08 \text{ g cm}^{-3}$. The substrate was uniformly mixed with slow-release fertilizer (Osmocote exact, N-P-K: 15–9–11; longevity of 8–9 months; Scotts Co., Marysville, Ohio, USA) at a concentration of 5 g L^{-1} . To avoid severe water stress, DCSs were watered 2–3 times a week until water dripped from the bottom of the containers. The volumetric water content at the field capacity level (24 h after watering) showed an increasing gradient along the container depth from $76\% \pm 0.8\%$ at a 0–10-cm depth to $86\% \pm 0.7\%$ at a 50–60-cm depth ($n = 5$), as determined by inserting an EC-5 sensor (Meter Group, Inc., Pullman, WA, USA) into containers filled only with coconut peat. As the cultivation period (November 2017–July 2018) was in dry season, the total rainfall was relatively small (260 mm), with maximum and minimum monthly mean temperatures of 33°C and 20°C , respectively (WorldClim data, n.d.).

Analysis of morphological traits

To analyze the morphological traits and root development of DCSs on the course of the cultivation in the nursery, five seedlings per species were randomly sampled at 1, 40–75, 120–155, and 180–215 days after transplantation (Table 1). The sampled shoots were cut at the cotyledon insertion point and separated into leaf and stem after measuring the shoot length and root collar diameter. The harvested leaves were scanned at 400 dpi optical resolution using a GT-S650 scanner (Epson, Nagano, Japan), and the surface area was calculated by pixel counting using the free software ImageJ

(Rasband 2012). The root ball was carefully removed from the container and cut into six round discs at 10-cm depth-sectional intervals until the bottom. The volume of each section, except for the top section, was approximately 500 cm³ (=16 cm² × 3.14 × 10 cm). The volume of the top section (0–10-cm depth layer) was approximately 400 cm³, as the top-most portion of the container (0–2-cm depth layer) was not filled with substrate. The harvested root ball sections were loosened in individual plastic trays, and all visible roots were manually detached from the substrate. The collected roots were cleaned with water and divided into suberized and absorptive roots upon visual inspection and texture sensation.

The roots were spread onto an A4 acrylic tray, submerged in water to minimize overlapping, and then scanned using the same methods as those used for the leaf area. The root length in each diameter class was calculated based on the scanned images of roots according to the method of Kimura and Yamasaki (2001). Tajima and Kato (2013) confirmed that the results obtained via this method correlated closely to those obtained using WinRHIZO commercial software (Coefficient of determination (R^2) > 0.95). Subsequently, the root lengths in each diameter class were grouped into three categories: fine ($0.35 < \phi < 1$ mm), medium ($1 < \phi < 4$ mm), and coarse ($\phi > 4$ mm). The biomass of all seedling fractions (stem, leaf, and root) was determined by weighing after drying in an oven at 74 °C for 4 days. SRL (cm g⁻¹) was then calculated based on the above measurements. The Dickson Quality Index (DQI) proposed by Dickson et al. (1960) was calculated according to the following equation:

$$\text{DQI} = (\text{shoot and root biomass [g]}) / [(\text{seedling length (cm)/collar diameter (mm)}) + (\text{shoot biomass (g)/root biomass (g)})]$$

DQI is an indicator of the quality of a seedling and is used to predict its field performance (Gallegos-Cedillo et al. 2021), considering their robustness and the balance between shoot and root biomass.

Statistical analysis

The growth model with the lowest Akaike information criterion (AIC) for shoot biomass, root biomass, total root length, and leaf area during the cultivation period was selected from the exponential, Gompertz, and three-parameter logistic models as the best predictive model (Paine et al. 2012). The growth rates (GRs) derived from the selected best growth models for the five species were compared in terms of the time period and magnitude of GR increase.

To evaluate vertical root development in the deep container, Generalized Linear Model (GLM) following gamma distribution with a log-link function was applied. The GLMs for each root growth parameter (root biomass, root length, and SRL) at the end of the cultivation period as response variables were examined with all possible groupings of the combinations of the root ball depth sections (0–10 cm to 50–60 cm) as explanatory variables. The best grouping of the root ball depth sections was determined by the GLM with the lowest AIC value (Crawley 2012). Furthermore, the best groupings for the total root biomass and length of fine, medium, and coarse roots at each sampling time were also selected in the same manner, by examining three root ball depth layers (top [0–20 cm], middle [20–40 cm], and bottom [40–60 cm], each 20 cm layer) as explanatory variables. All statistical analyses were performed using R version 4.0.1 (R Core Team 2020).

RESULTS

Root growth and morphology in DCSs at the end of the cultivation period

All tree species developed roots to the bottom of the container without spiraling by the end of the cultivation period (Fig. 2). However, the vertical distribution of the root on the root ball surface showed slightly different patterns among species (Fig. 2).

Total root length per root ball section tended to increase with container depth for all tree species (Figs 3 a–e). The total root length in the deepest section (50–60-cm depth) exceeded 800 cm, equivalent to $> 1.6 \text{ cm cm}^{-3}$, for all species (Figs 3 a–e). Conversely, the total root biomass per root ball section tended to decrease gradually with depth for all species except *H. crenulata* (Figs 3 f–j). SRL, an index of the root branching degree and the nutrient and water uptake rates, tended to increase with depth, similar to the total root length (Figs 3 k–o). SRL of *A. indica* and *T. indica* increased drastically at the deepest section (50–60-cm depth), while those of the other species gradually increased along the depth gradient.

Vertical root development in the DCS during the cultivation period

Vertical root development in the DCSs showed both common and species-specific temporal patterns during the cultivation period (Fig. 4). At the early phase of the cultivation period (until approximately 60 days after transplantation),



Fig. 2. Root balls of deep-container seedlings at the end of the cultivation period. The figures beside each root ball section indicate the total root length at each depth section.

none of the species had developed coarse roots at any depth layer (Figs 4 k-o). All species formed long, fine roots in the bottom layer by the end of the cultivation period (Figs 4 a-e), and the bottom layer was almost entirely occupied by fine roots (Figs 4 a-o). The total length of medium roots was the shortest in the top layer for all species (Figs 4 f-j) except *E. camaldulensis*.

According to their species-specific characteristics, only *A. indica* and *T. indica* developed coarse roots (9.6 ± 3.7 cm and 1.6 ± 1.3 cm in length, respectively) in the bottom layer by the end of the cultivation period (Figs 4 k and l); whereas, the other species developed almost no coarse roots in that layer (Figs 4 m-o). *E. camaldulensis* developed fine roots with a total length of >500 cm in the bottom layer within 60 days of transplantation (Fig. 4e). *T. hamiltoniana* developed no coarse roots (almost 0 cm in length) in the middle and bottom layers within the

cultivation period (Fig. 4n), but rapidly developed medium roots in both these layers from 140–200 days after transplantation (Fig. 4i).

Aboveground and belowground DCS growth during the cultivation period

The cumulative growth (CG) of shoot biomass, root biomass, root length, and leaf area showed variable temporal patterns among species (Figs 5 a-d). At the end of the cultivation period (180–215 days after transplantation), the total growth of these parameters was as follows: CG of the shoot biomass was highest for *E. camaldulensis* and lowest for *H. crenulata* (Fig. 5a), CG of the root biomass was highest for *A. indica* and *T. indica* (Fig. 5b), CG of the root length was highest for *T. hamiltoniana* (Fig. 5c), and CG of the leaf area was highest for *A. indica* and *T. indica* (Fig. 5d).

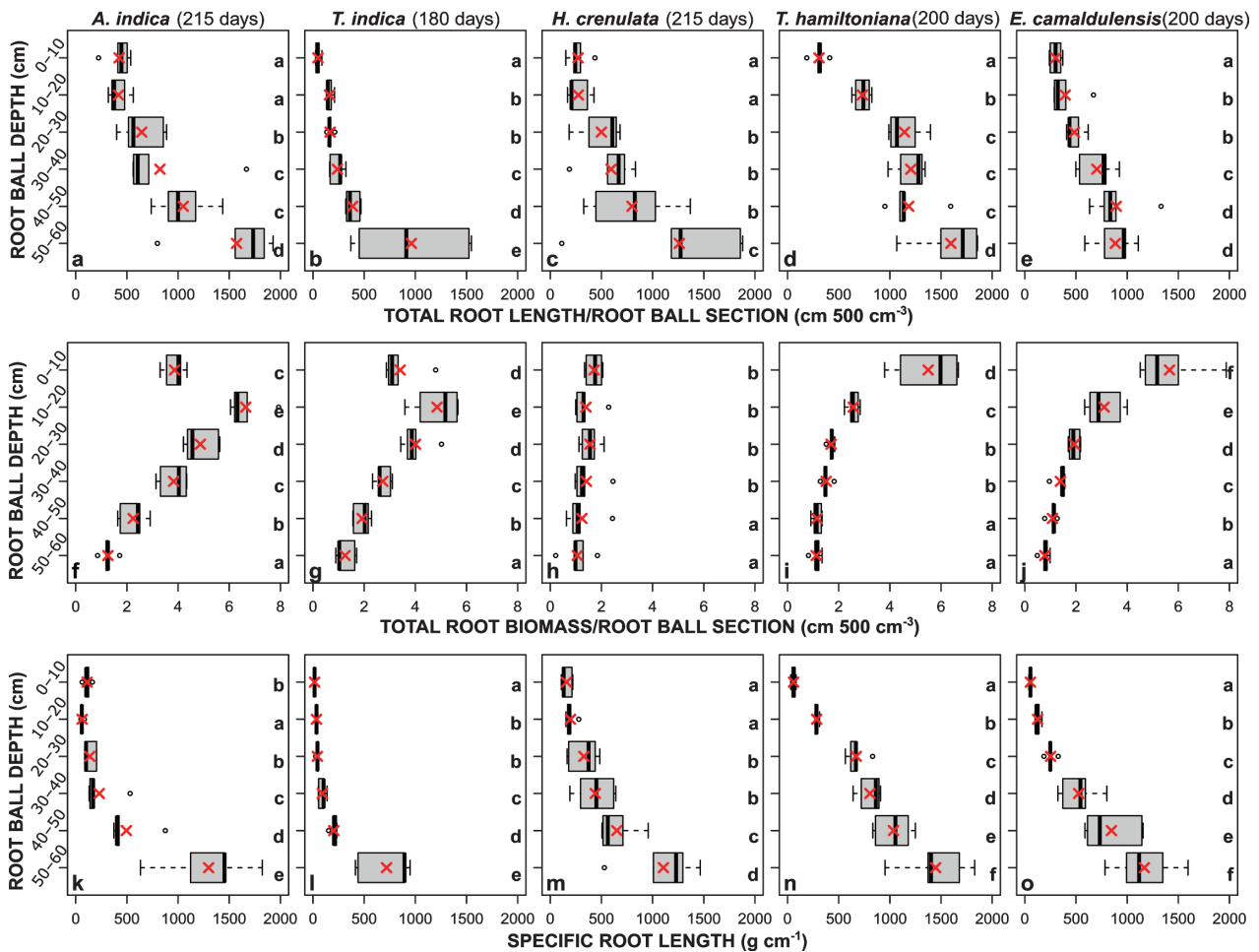


Fig. 3. (a–e) Total root length, (f–j) total root biomass, and (k–o) specific root length according to the root ball depth at the end of the cultivation period. The boxes indicate the 25th and 75th percentiles, solid lines indicate the median, whiskers indicate the 5th and 95th percentiles, and crosses indicate the mean value ($n = 5$). Different letters indicate differences in root morphology (traits) based on the grouping of the root ball depth sections with model selection by a generalized linear model (GLM). Although the actual volume of the top root ball section (0–10 cm) was 400 cm³, the values for that section were converted to 500 cm³ for easy comparison with the volumes of other sections.

The GRs derived from the CG for each growth parameter also showed species-specific characteristics (Figs 5e–h). For *E. camaldulensis*, an introduced evergreen species, all four GRs tended to reach a peak earlier than those of the other tree species. In contrast, for *H. crenulata*, all four GRs tended to reach a peak later than those for the other tree species, and in an almost synchronized manner. For *A. indica*, *T. indica*, and *T. hamiltoniana*, the GR of root biomass continuously increased after the peak of the GR of shoot biomass (Fig. 5f). The GR of root length of *H. crenulata* and *T. hamiltoniana*, both of which are indigenous deciduous species, exhibited a similar pattern with a continuous increase in GR of root length until late in the cultivation period (Fig. 5g). The GR of root length of *H. crenulata* was almost synchronized with the shoot and root biomass and leaf area GR; whereas, the peak of the GR of

leaf area occurred earlier than the other three growth parameters in the case of *T. hamiltoniana* (Fig. 5e–h).

The DQI of the five species increased over the cultivation period (Fig. 6). *H. crenulata* consistently showed the lowest DQI among the five species during the cultivation period.

DISCUSSION

Eligibility of tropical dry forest species for cultivation in deep containers

To maximize the benefit of the deep-rooting potential of DCSs after outplanting, it is essential that the roots reach the bottom of the deep container during the nursery period.

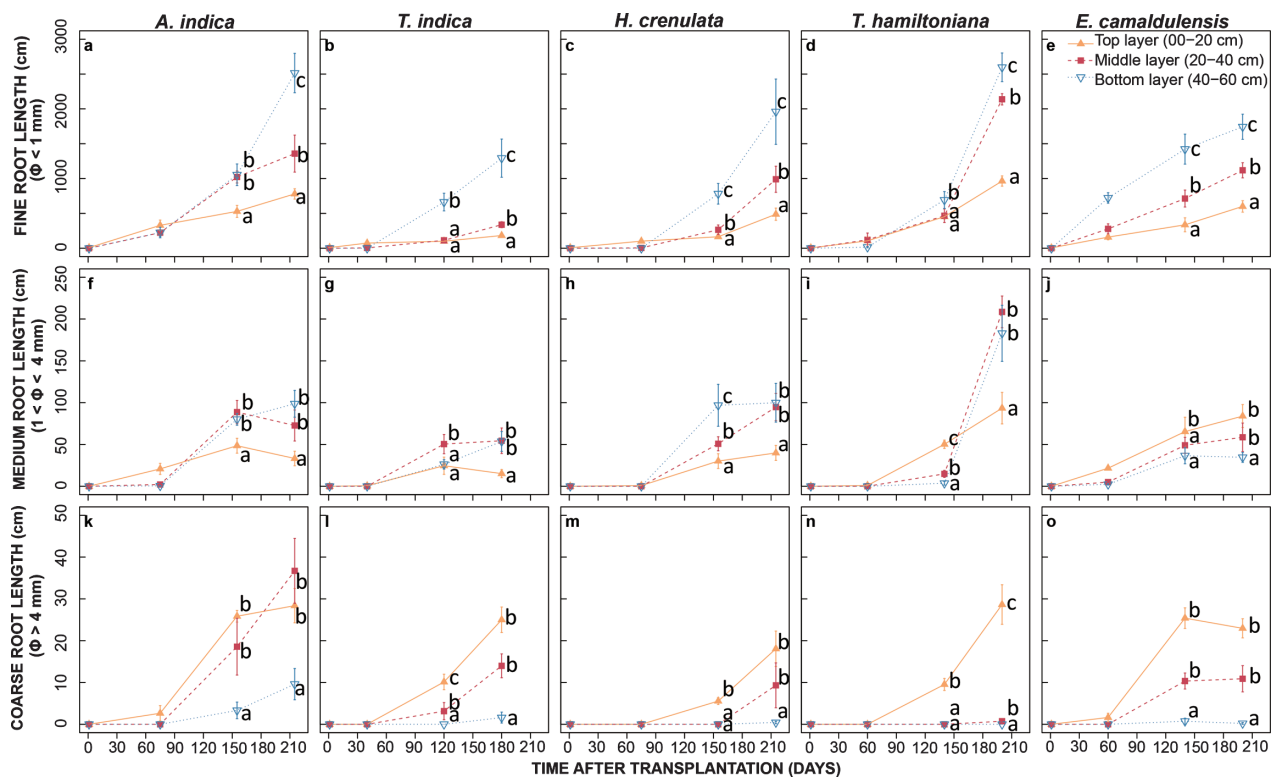


Fig. 4. Development of the total length of the: (a–e) fine, (f–j) medium, and (k–o) coarse roots, presented by the root ball depth layer (top, middle, and bottom) during the cultivation period. Values are the mean $\pm$ standard error ($n = 5$). Different letters indicate differences in root growth at each sampling time based on the grouping of the root ball depth layers with model selection by a generalized linear model (GLM). Although the actual volume of the top layer (0–20 cm) was 900 cm³, the values were converted to the 1,000 cm³ level to facilitate easy comparison with the volumes of other layers.

We demonstrated that the five tropical dry forest species developed roots with a total length of > 800 cm in the deepest container section (50–60-cm depth) within the cultivation period (approximately 200 days) under well-watered conditions in the whole container (Figs 3 a–e).

Our results suggested that tropical dry forest species can rapidly develop root systems during a short nursery period, which is preferable for DCS cultivation. In the case of Mediterranean tree species, *Quercus ilex* (100-cm-depth container) was successfully grown during a single growth period (Pemán et al. 2006); whereas, *Q. robur* and *J. regia* (60-cm-depth container) required 2 years for roots to grow to sufficiently deep levels, even under well-watered conditions (Mariotti et al. 2015a). In another experiment, the taproots of *Acacia cavan* in Chile did not reach the bottom of a 45-cm-deep container within a 6-month cultivation period (De La Fuente et al. 2017).

Furthermore, all of the five tested species had DQI > 2.4 (Fig. 6), which was higher than the reported values for DCSs of Mediterranean species, such as 2.35 ± 0.66 for *Quercus suber* L. (Chirino et al. 2008) and 0.18 ± 0.02 for *Acacia caven* (De La Fuente et al. 2017). Hence, the tropical

dry forest species analyzed herein may be suitable for DCS production, since their roots developed adequately in the deep container layers without excessive shoot growth under an ordinary nursery cultivation regime (full sunlight, well-watered condition, and common substrate).

Root development of tropical dry forest species in deep containers

In the present study, a common characteristic of the five species with different leaf phenologies was an increase in SRL and fine root length with increasing container depth (Figs 3 a–e and k–o). Although we raised the DCSs without severe water stress, a moisture gradient was formed from the top to the bottom layer due to immediate drainage under gravitational force following watering (Landis and Nisley 1990). Under such conditions, all of the five species could extend roots toward the bottom of the container and develop a relatively dense fine root in the deepest section where water availability was highest. This suggested the common adaptive strategy of these tropical dry forest species to explore and utilize water resource in the deep soil layer

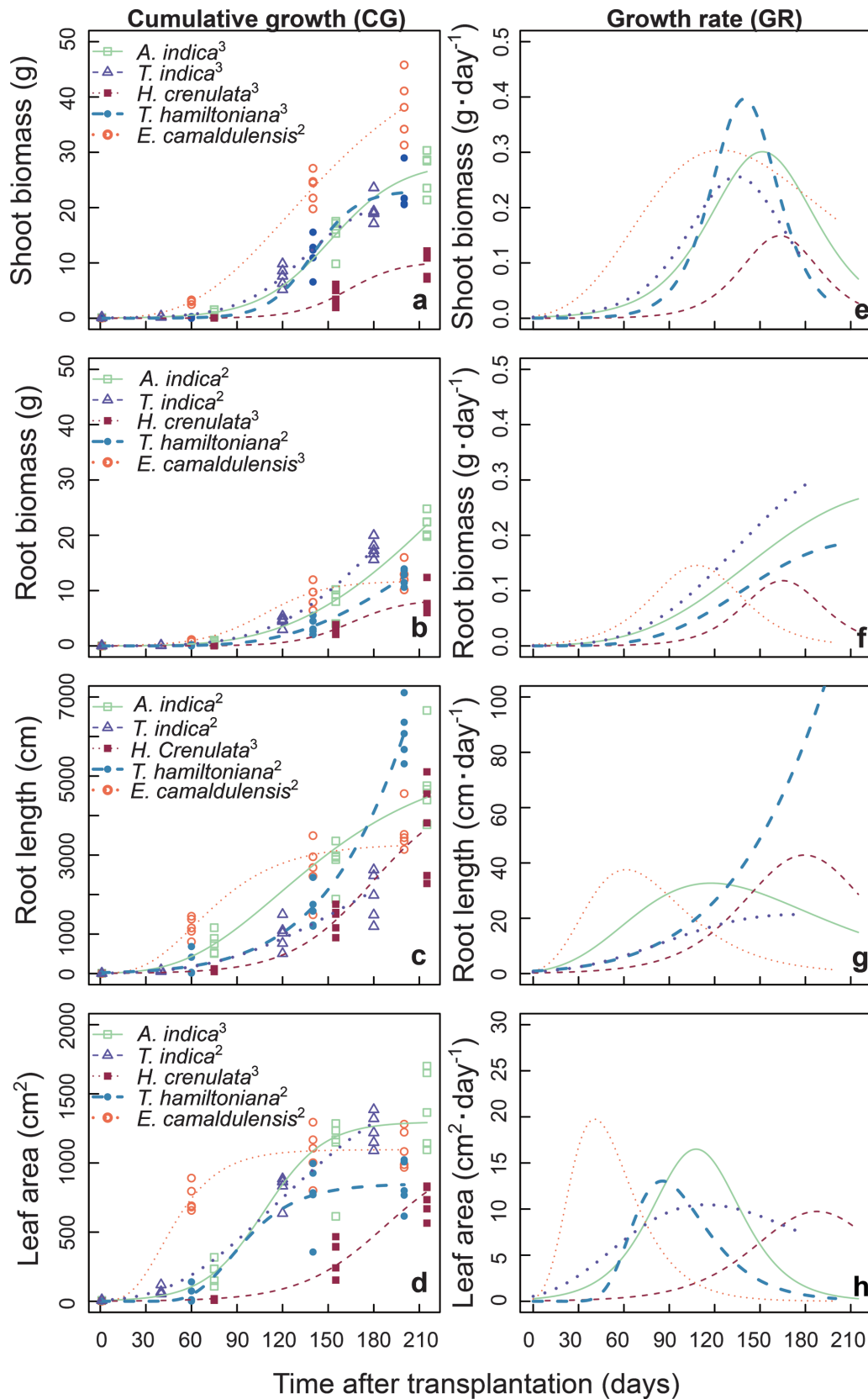


Fig. 5. (a–d) Cumulative growth (CG) and (e–h) growth rate (GR) of (a, e) shoot biomass, (b, f) root biomass, (c, g) root length, and (d, h) leaf area during the cultivation period including initial size at transportation. Only the models with the lowest Akaike information criterion are shown, selected from the exponential¹, Gompertz², and three-parameter logistic³ models (the exponential model was not selected in any case). $n = 5$ for each sampling.

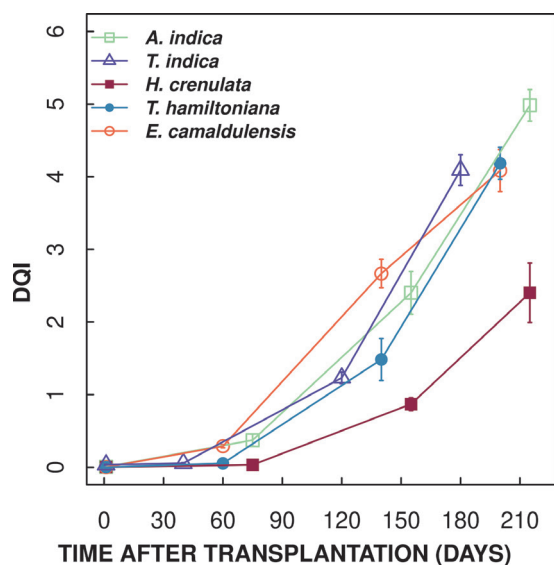


Fig. 6. Dickson quality index (DQI) during the cultivation period. Values are the mean $\pm$ standard error ($n = 5$)

(Brunner et al. 2015; Olmo et al. 2014; Padilla and Pugnaire 2007).

These root growth patterns are consistent with those reported by Boonman et al. (2020), who grew 24 tropical tree species (representing African dry savanna, humid savanna, and dry and moist forest species) in 100-cm-deep plastic tubes for 6 months without water stress. It was observed that the roots of dry forest species showed higher SRL (fine root development) in the deeper section (50–75-cm depth) than in the top section (0–25-cm depth). Several studies have shown the high plasticity of the root growth habit of drought-tolerant tree species in increasing the rooting depth (Reader et al. 1993), total root length (Padilla and Pugnaire 2007), and SRL (Padilla et al. 2009) under moderate drought conditions. Vertical root development to explore water availability in the deep layer even without severe water stress could be considered a common adaptation strategy of tropical dry forest species to drought.

Species-specific growth and biomass allocation patterns of DCSs

In the present study, we raised DCSs under well-watered conditions with the expectation that the selected dry forest tree species would show intrinsic trait differences, originating from long-term environmental filtering and/or evolutionary processes, which allow species to adapt to that environment (Boonman et al. 2020). We could then observe species-specific patterns of root growth and biomass allocation among five tropical dry forest species grown in deep containers. This implied that each species potentially

employs a different strategy at the nursery stage as an adaptation to drought during the dry season.

E. camaldulensis showed the earliest increase in the GR of leaf area and root length, which peaked approximately 60 days after transplantation (Figs 5 g and h). Furthermore, this species rapidly developed fine roots in the bottom layer early in the cultivation period (Fig. 4e). *E. camaldulensis*, native to Australia, is known globally as a fast-growing plantation species in tropical arid regions (Ugalde and Pérez 2001). It has been reported that *E. camaldulensis* has a deeply branched root system with both lateral and tap/sinker roots capable of absorbing water in deep soil layers (Burgess et al. 1998; Pereira and Kozłowski 1976). The observed development of long medium roots with a total length of almost 100 cm in the top layer (Fig. 4j) and coarse roots in the middle layer (Fig. 4o) may have reflected this unique root habit as a drought adaptation strategy to utilize a wide range of water resources.

While deciduous species avoid drought stress by defoliation, evergreen species are drought-tolerant with high biomass allocation to the root, deep taproot formation, and high SRL (Brunner et al. 2015; Markesteijn and Poorter 2009). *A. indica* and *T. indica*, both of which are localized evergreen species (Thein and Ba 2005), had higher root biomass than the other species (Figs 3f, 3g, and 5b) and developed coarse roots ($\phi > 4$ mm) down to the bottom layer of the container (Figs 4k and l) and distinctly fine roots in the deepest section of the container (Figs 3k and l). Most of these coarse roots can be considered taproots, a specialized root system in many dry forest species used for accessing and transporting water from the deep soil layer (Canadell et al. 1996). The habit of elongating taproots deep into the soil has been also observed in the field in these two species (Das and Chaturvedi 2008; El-Siddig et al. 2006).

H. crenulata and *T. hamiltoniana*, both of which are indigenous deciduous species in Myanmar, exhibited a similar pattern with a slow increase in CG of root length during the cultivation period. As deciduous species can avoid water stress by shedding leaves (Markesteijn and Poorter 2009), these two species may not exhibit the strategy of developing roots as rapidly as the other three evergreen-type species. Slow growth of shoot biomass for *H. crenulata* can also be considered an adaptation to drought. In contrast, *T. hamiltoniana* rarely developed coarse roots (e.g., a taproot was observed even in the middle layer; Fig. 4n) but did develop medium roots (e.g., lateral root and fine roots branched from the top layer; Figs 4d and i). *Tectona grandis*, a closely related species but native to moister habitats than *T. hamiltoniana* in Myanmar

(FAO 1986), is known to develop a shallow root system to a depth of only approximately 60 cm, even 19 years after outplanting (Srivastava et al. 1986). Since shallow-rooted deciduous species with fine roots concentrated down to a 40-cm depth are also found in seasonally dry forests (Ovalle et al. 2015), *T. hamiltoniana* may be a type of shallow-rooted dry forest species.

Application of M-StAR containers for DCS production in tropical dry forest

M-StAR containers have several merits such as high size flexibility, operational efficiency, and low cost for DCS production. Utilizing M-StAR containers could promote the application of the DCS technique for dryland reforestation in developing countries, where vinyl pot seedlings remain popular. In addition, we demonstrated that DCSs can be grown well in 100 % coconut peat, which has merits such as lighter specific weight and higher air content than peat moss (Abad et al. 2005); however, DCSs have been grown in peat moss (Sagrera et al. 2013), sand (Pemán et al. 2006), and a substrate mixed with coconut peat (Chirino et al. 2008; Mariotti et al. 2015a, b). Our findings could further facilitate the widespread adoption of the DCS technique in tropical countries where coconut peat is readily available.

CONCLUSIONS

In the present study, we examined the suitability of common tropical dry forest species for DCS cultivation in M-StAR containers focusing on vertical root development. We found that all examined species successfully developed roots down to the bottom of the containers with a high DQI within approximately 200 days. These five species showed gradual increases in total root length and SRL with increasing container depth, thereby enhancing the ability to utilize water deep in the soil. This may be a characteristic shared by tropical dry forest species, although the pattern of vertical rooting of coarse and medium roots and the shoot biomass allocation varied among the species.

These findings indicated the large potential of the DCS cultivation technique with M-StAR for other tropical dry forest species. However, different rooting strategies identified in the present study may affect the future survival and growth of the planted seedlings in the field. To apply the DCS technique to practical dryland restoration, the field performance of DCSs should be further evaluated in future research.

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Disclosure statement

The authors report there are no competing interests to declare.

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Data availability statement

The data that support the findings of this study are available from the corresponding author.

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