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Physiology of Santalum Album L. Seedlings: Impact of Host Varieties and Potting Mixture Diversity

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Abstract

Santalum album L., commonly known as sandalwood, holds significant importance due to its diverse applications in industries such as perfumery and pharmaceuticals. As a hemi-parasitic species, it forms essential nutritional connections with the roots of various host plants, influencing its physiology. An experiment was conducted to investigate how different host plants and potting mixtures, enriched with mycorrhizae, impact the physiological characteristics of sandalwood seedlings during the nursery stage. Three primary host plants (*Albizia lebbeck*, *Casuarina junghuniana*, and *Alternanthera sessilis*) were considered as main plot treatments, while various potting mixtures (nine sub-plot treatments: potting mixture with mycorrhizae in the standard ratio of sand soil, farmyard manure, burnt rice husk and vermicompost) were examined in a split-plot experiment with replicates. Measurements of CO_2 assimilation rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate were taken at intervals after transplanting (90, 180, and 270 days). The CO_2 assimilation rate and intercellular CO_2 concentration with the host plant *Casuarina junghuhniana* were found to be 2.25 µmol CO_2 m^{-2} s^{-1} and 316.73 µmol CO_2 mol^{-1}, respectively. Physiological parameters indicated better growth with combinations of burnt rice husk, soil, and farmyard manure. Sandalwood seedlings grown with the host plant *C. junghuhniana* and a potting mixture consisting of burnt rice husk, soil, and farmyard manure, either alone or in combination with arbuscular mycorrhizalstrains (*Glomus fasiculatum* and *Glomus intraradices*), exhibited superior physiological performance. The study revealed that the choice of host plant and potting mixture significantly influenced the physiological performance of sandalwood seedlings. These findings accentuate the importance of selecting appropriate host varieties and potting mixtures to optimize the growth and physiological responses of *S. album* seedlings in nursery settings.

Keywords: Assimilation rate, Haustoria, Host, stomatal conductance, transplant.

Introduction

Indian sandalwood (*Santalum album* L.) stands as a beacon of economic prosperity within the forestry sector, revered for its esteemed value and myriad applications. With prices ranging from Rs. 5000 to Rs. 12000 per kilogram based on quality, the allure of this botanical treasure persists unabated. The market trajectory tells a compelling tale of escalating worth, with sandal heartwood prices witnessing a remarkable ascent over the years. From a modest Rs. 365 per ton in 1900, the value surged to Rs. 6.5 lakhs per ton in 1999-2000, further soaring to Rs. 37 lakhs per ton in 2007 and an astounding Rs. 56.5 lakhs per ton in 2012 (Arun Kumar *et al.*, 2012). This exponential rise emphasizes not only the enduring demand for sandalwood and its derivatives but also the dwindling supplies that beckon urgent attention.

As the clamor for sandalwood and its precious oil intensifies, the reality of diminishing resources looms large (Bunney *et al.*, 2022). Sandalwood populations have been significantly reduced due to historical overharvesting, poor management, and illegal logging (Roa *et al.*, 2016; Rashkow, 2022). The establishment of sandalwood plantations provides an alternative resource, but remaining wild populations are still under threat (Page *et al.*, 2010). Stringent regulations and policies have been put in place to prevent illegal harvest, but enforcement is hindered by a lack of forensic tools to verify the origin and quality of sandalwood products (Bunei, 2017).To address this pressing issue, expanding the cultivation of sandalwood on a commercial scale becomes imperative. Yet, the pathway to increased cultivation is fraught with challenges, chief among them being the production of high-quality planting stock. In the pursuit of broadening the coverage of sandalwood cultivation, the quality of planting material assumes paramount importance, necessitating meticulous assessment of both morphological and physiological parameters.

The physiology of *S. album* L. seedlings emerges as a focal point in this endeavor, serving as a linchpin in the quest for sustainable cultivation practices. Within this context, the impact of host varieties and potting mix diversity on the physiological attributes of sandalwood seedlings assumes critical significance. By probing into the complex interaction between host plants and potting mixtures enriched with mycorrhizae, researchers seek to unravel the nuanced dynamics that govern the growth and development of sandalwood seedlings during their formative nursery stage (Cowden *et al.*, 2019). The exploration of adaptive forest management strategies represents a crucial step forward in mitigating the challenges posed by climate change (Nagel *et al.*, 2017). As environmental shifts continue to exert profound impacts onforest ecosystems, the need for adaptive measures becomes increasingly urgent.Furthermore, coexisting tree species with different functional traits may have inconsistent responses to warming and decreased precipitation, leading to species distribution shifts and changes in community dynamics (Bussotti and Pollastrini, 2021). In this regard, understanding the physiological responses of sandalwood seedlings to varying environmental conditions holds profound implications for boosting their resilience in the face of climate variability. Studies have shown that different tree species exhibit variation and plasticity in stress hydraulic parameters, such as photosynthetic capacity and quantum efficiency of photosystem II, which are beneficial for displaying physiological responses at the leaf level (Vicente, 2022).Hence, the present studyto investigate how different host plants and potting mixtures, enriched with mycorrhizae, impact the physiological characteristics of sandalwood seedlings during the nursery stagecultivation unfolds against a backdrop of evolving market dynamics and environmental imperatives. As stakeholders navigate the complexities of supply and demand, the imperative of enhancing cultivation practices assumes paramount importance.

Methods

This experiment took place during 2019-20 at the nursery of the College of Forestry, Ponnampet, situated in the hilly region (Zone 9) of Kodagu district, Karnataka. Ponnampet's coordinates are approximately 120° 20' N latitude and 75° 56' E longitude, with an altitude of 867 meters above sea level. In this study, 27 different combinations were tested, comprising three host plants (*Albizia lebbeck*, *Casuarina junghuhniana* and *Alternanthera sessilis*), three types of potting mixtures, and two types of Vesicular Arbuscular Mycorrhizal (VAM) fungi (*Glomus fasiculatum* and *Glomus intraradice*). Host were taken as the main plot treatments - *Albizia lebbeck*(H1), *Casuarina junghuhniana*(H2) and *Alternanthera sessilis* (H3). The potting mixture with VAM combination were taken as sub-plot treatments - Sand+Soil+FYM + Control(T1), Sand+Soil+FYM+*Glomusfasiculatum*(T2), Sand+Soil+FYM+*Glomus intraradices*(T3), Burnt rice Husk+Soil+FYM + Control(T4), Burnt rice Husk+Soil+FYM +*Glomus fasiculatum*(T5), Burnt rice Husk+Soil+FYM +*Glomus intraradices*(T6), Sand+Soil+Vermicompost + Control(T7), Sand+Soil+Vermicompost + *Glomus fasiculatum*(T8) and Sand+Soil+Vermicompost + *Glomus intraradices*(T9)

The experimental design utilized a split-plot layout, with the host plants as the main plots and the potting mixtures with VAM fungi as the sub-plot treatments. There were three main plots and nine sub-plots in total. Each treatment was replicated three times, with 30 plants per replication, totaling 90 plants per treatment. Physiological measurements were taken at 90 and 270 days after transplanting the sandalwood seedlings, using the CICAS-3 Portable Photosynthesis System. Five seedlings were randomly selected from each treatment for the analysis. Measurements were conducted on healthy, fully expanded leaves in the middle third of each treatment, during daylight hours with solar luminosity conditions between 10 am and 12 pm. Weather conditions, including maximum and minimum temperatures, and relative humidity, were recorded at 90 and 270 days after transplanting (24.10°C, 19.22°C, 94.00% and 33.26°C, 15.94°C, 92.00% respectively). The leaf chamber of the photosynthetic meter was set at 380 ppm CO2, with a temperature of 24°C, and a saturating photosynthetic rate of 1500 μmol $m^{-2}s^{-1}$.

The observations were recorded for several physiological parameters, including CO_2 assimilation rate (A), stomatal conductance (gs), transpiration rate (E), and intercellular CO_2 concentration (Ci). The CO_2 assimilation rate was measured in μmol CO_2 m^{-2} s^{-1}, stomatal conductance was expressed in mol H_2O m^{-2} s^{-1}, transpiration rate was recorded in mmol H_2O m^{-2} s^{-1}, and intercellular CO_2 concentration was quantified in μmol CO_2 mol^{-1}.Afterwards, Water Use Efficiency (WUE), calculated as the ratio of CO_2 assimilation rate (A) to transpiration rate (E), and Instantaneous Carboxylation Efficiency (iCE), determined by the ratio of CO_2 assimilation rate (A) to intercellular CO_2 concentration (Ci), were computed and analyzed based on the observed physiological parameters. All the observations recorded were analyzed as per the procedure of Jayaraman (2001). The data were subjected to analysis of variance (ANOVA) on split plot design using SPSS software package after square root transformation of proportions and count data.

Results

Physiological parameters

The CO_2 assimilation rate was highest after 90 days of transplantation with *C. junghuhniana* (H2), reaching 1.78 μmol CO_2 m^{-2} S^{-1}, followed by *A. sessilis* (H3) at 1.70 μmol CO_2 m^{-2} S^{-1}. Among the sub-treatments, the highest rate was observed in burnt rice husk, soil, FYM, and G. *fasiculatum* (T5) at 2.18

µmol CO_2 m^{-2} S^{-1}, while the lowest rate was recorded with burnt rice husk, soil, and FYM (T4) at 1.21 µmol CO_2 m^{-2} S^{-1}. In the interaction effect, the highest rate was found in H3*T5 (2.43 µmol CO_2 m^{-2} S^{-1}), while the lowest values were observed in the combinations H1*T4 (0.67 µmol CO_2 m^{-2} S^{-1}) and H3*T8 (0.70 µmol CO_2 m^{-2} S^{-1}). After 270 days, the highest CO_2 assimilation rate was observed with H2 (2.25 µmol CO_2 m^{-2} S^{-1}), followed closely by H1 (2.24 µmol CO_2 m^{-2} S^{-1}). Among the sub-plot treatments, the highest rate was recorded in T4 (2.78 µmol CO_2 m^{-2} S^{-1}), while the lowest was observed in T2 (1.67 µmol CO_2 m^{-2} S^{-1}).

Similarly, stomatal conductance initially showed higher values with *C. junghuhniana* (H2) at 75.94 $molH_2Om^{-2}S^{-1}$, followed by *A. sessilis* (H3) at 60.91 $molH2Om^{-2}S^{-1}$. Among the potting mixtures, sand, soil, FYM (T1) displayed the highest stomatal conductance at 88.67 $molH_2Om^{-2}S^{-1}$. The interaction showed the highest stomatal conductance in H3*T1 at 143.00 $molH_2Om^{-2}S^{-1}$ and the lowest in H1*T3 at 27.53 $molH_2Om^{-2}S^{-1}$. After 270 days, the highest stomatal conductance was observed with H3 at 66.13 $molH_2Om^{-2}S^{-1}$, with the highest rate recorded in T3 (60.38 $molH_2Om^{-2}S^{-1}$) among the sub-plot treatments. The interaction showed the highest stomatal conductance in H3*T4 at 98.00 $molH_2Om^{-2}S^{-1}$ and the lowest in H1*T7 at 24.00 $molH_2Om^{-2}S\text{-}^{1.}$

Intercellular CO_2 concentration initially showed higher values with *C. junghuhniana* (H2) at 316.73µmol CO_2 mol-^{1}. The highest concentration was observed with burnt rice husk, soil, and FYM (T4) at 337.22 µmol CO_2 mol^{-1}. The interaction showed the highest concentration in H1*T7 at 422.00 µmol CO_2 mol^{-1} and the lowest in H1*T3 at 237.80 µmol CO_2 mol^{-1}. By the end of the experiment, the highest concentration was observed with *A. sessilis* (H3) at 295.85 µmol CO_2 $mol^{-1.}$ The highest concentration among sub-plot treatments was observed with sand, soil, vermicompost, and *G. fasiculatum* (T8) at 320.44 µmol CO_2 mol^{-1}. The interaction showed the highest concentration in H3*T9 at 336.40 µmol CO_2 mol-1 and the lowest in H1*T4 at 214.67 µmol CO_2 mol^{-1}.

Transpiration rate was initially higher with *C. junghuhniana* (H2) at 1.39 mmol H_2O m^{-2} S^{-1}, with the highest rate recorded in T4 (1.53 mmol H_2O m^{-2} S^{-1}) among sub-plot treatments. The interaction showed the highest rate in H1*T7 at 2.55 mmol H_2O m^{-2} S^{-1} and the lowest in H1*T3 at 0.60 mmol H_2O m^{-2} S^{-1}. After 270 days, the highest rate was observed with H3 at 1.60 mmol H_2O m^{-2} S^{-1}, with the highest rate recorded in T3 (1.50 mmol H_2O m^{-2} S-1) among sub-plot treatments. The interaction showed the highest rate in H3*T4 at 2.53 mmol H_2O m^{-2} S^{-1} and the lowest in H2*T1 at 0.56 mmol H_2O m^{-2} S^{-1}.

Water use efficiency (WUF) and Carboxylation efficiency (CE)

Initially, higher water use efficiency (WUE) was observed with pot host *A. lebbeck* (H1) at 2.05, followed by *A. sessilis* (H3) at 1.84. Among the subplot treatments, seedlings grown in potting mixture sand, soil, FYM, and *G. intraradices* (T3) had higher WUE at 2.41, followed by those with sand, soil, FYM (T1) at 2.34. Conversely, the least WUE was recorded with burnt rice husk, soil, and FYM (T4) at 1.07. The interaction effect on WUE revealed that the highest WUE was with H1*T1 combination at 4.53, followed by H2*T8 combination at 3.90. Conversely, the least WUE was recorded with H1*T7 at 0.49 and H1*T4 at 0.67.

Finally, after 270 days of transplanting, higher WUE was recorded with pot host *C. junghuhniana* (H2) at 2.62, followed by *A. lebbeck* at 2.39. In the subplot treatment, seedlings with T1 had higher WUE at 3.48, while the least was noticed with sand, soil, vermicompost, and *G. fasiculatum* (T8) at 1.54. In the interaction effect of host plants and treatment, seedlings with H1*T7 treatment had higher WUE at 5.87, followed by H3*T1 at 4.32 and H2*T1 at 3.84. Conversely, the least was recorded in H3*T6 at 0.97 and

H3*T3 at 1.19. Regarding carboxylation efficiency, it remained consistently low across all treatments even after 270 days of transplanting, with a value of 0.01. However, it slightly increased to 0.02 for the interaction of H1*T4 and H2*T1.

Discussion

Understanding the physiological processes governing plant systems is crucial for assessing their growth and development across various stages. Processes such as CO_2 assimilation directly impact biomass accumulation, influencing plant health and productivity. In sandal seedlings, physiological variables exhibit significant fluctuations regardless of treatment. After 90- and 270-days post-transplantation, CO_2 assimilation rates were notably higher with the host *C. junghuhiana* (H2) at 1.78 µmolCO_2 m^{-2} S^{-1} and 2.25 µmolCO_2 m^{-2} S^{-1}, respectively. This is likely due to nutrient supply from host plants, influencing seedling intercellular activity. The combination of burnt rice husk, soil, FYM, and *G. fasciculaltum* also enhanced CO_2 assimilation at 2.18 µmolCO_2 m^{-2} S^{-1}, accompanied by notable leaf growth.The addition of burnt rice husk to soil has been found to enhance porosity and moisture retention capacity, leading to improved plant growth and increased CO_2 assimilation (Sy et al., 2021; Kim, 2023). Similar to the present results, the application of burnt rice husk, lime, and phosphorus fertilizer has been shown to increase soil pH, phosphorus availability, and nutrient uptake in maize plants, resulting in increased CO_2 assimilation and higher yields (Sy et al., 2021). The use of biochar, including burnt rice husk, has also been found to reduce greenhouse gas emissions, such as CH4 and N2O, from paddy fields, further contributing to the mitigation of climate change (Mosharrof et al., 2021; Kim, 2023). Overall, the combination of burnt rice husk, soil, FYM, and *G. fasciculatum* can positively impact CO_2 assimilation in plants through improved soil properties, nutrient availability, and reduced greenhouse gas emissions.

Interaction between *A.sessilis* and the same potting mixture further increased CO_2 assimilation to 2.43 µmolCO_2 m^{-2} S^{-1}. Conversely, lower CO_2 assimilation rates in sandalwood seedlings of 1.21µmolCO_2 m^{-2} S^{-1} were observed with burnt rice husk, soil, and FYM, likely due to insufficient nutrient supply (Fleischer and Terrer, 2022). Additionally, ithe decomposition of organic sources, including rice straw, rice-straw-derived biochar and compost, rice husk, rice husk ash, and farmyard manure, was studied by Benbi and Yadav (2015), and it was found that carbon mineralization was greater from rice straw and rice husk compared to other sources. These findings suggest that the lower CO_2 assimilation rates observed in sandalwood seedlings with burnt rice husk, soil, and FYM may be attributed to the inadequate nutrient supply provided by these materials (Carswell 1998; Carswell et al., 2000).The present findings align with Dalmolin et al. (2015), supporting similar observations in coffee plant nursery stages. Moreover, Alcántara et al. (2019) suggest that low intercellular CO_2 concentrations enlarge stomatal openings, increasing carbon assimilation rates.

Sandal seedlings grown along with *C. junghuhniana* had higher stomatal conductance (75.94 molH_2Om^{-2}S^{-1}) and the sub treatment sand, soil and FYM without AM fungi expressed higher stomatal conductance (88.67 molH_2Om^{-2}S^{-1}), after 90 days of transplanting. The results could be attributed to higher CO_2 assimilation in case of *C. junghuhniana* as pot host. Similar observations were recorded by Rocha *et al.* (2014) when sandalwood was planted with *Casuarina equisetifolia* as host plants and it was found that sandal trees showed higher carbon assimilation rate, higher pre-dawn plant water potential, and higher leaf nutrient content. The host plant supplements the nutrient requirements of sandal trees through haustoria connections, and the most outstanding influence can be observed in increasing the potassium (K) status of the sandal tree (Lamour *et al.,* 2023). Therefore, the presence of *C.*

junghuhniana and the addition of sand, soil, and FYM without AM fungi likely contributed to the higher stomatal conductance observed in the sandal seedlings after 90 days of transplanting (Stefanski *et al.*, 2023).It was also higher, with interaction of same host and potting media (143.00 $molH_2Om^{-2}S^{-1}$) (Fig A.3). However, as plants grew in height, stomatal conductance decreased in pot host *C. junghuhniana* (41.61$molH_2Om^{-2}S^{-1}$). The decrease in stomatal conductance after 270 days of transplanting could be possibly due to a lower CO_2 assimilation rate caused by stomata closure and CO_2concentration within the sub-stomatic chamber, impairing activities in the photosynthetic apparatus (Taiz *et al.*, 2017).

Intercellular CO_2 concentration was higher with primary host *C. junghuhiana*(316.73µmol CO_2 mol^{-1}) and with potting mixture combination of burnt rice husk, soil and FYM without AM fungi (337.22 µmol CO_2 mol^{-1}), after 90 days of transplanting. The addition of burnt rice husk in the potting media has been shown to increase the movement of carbon in the mesophyll of leaves, leading to increased accumulation of intercellular carbon and higher metabolic activity in the above case (Linam *et al.*, 2022). Additionally, Quintero *et al.* (2011)opined that the use of burnt rice husk as a substrate has been found to affect the physicochemical characteristics of the substrate throughout the crop cycle, including changes in pH, cation exchange capacity, and exchangeable cations. These findings suggest that the addition of burnt rice husk can have a positive impact on the movement of carbon and metabolic activity in sandalwood plants, potentially leading to improved growth and development. Further, the least was noticed with the same potting mixture with AM fungi *G. Fasciculatum* (261.22 µmol CO_2 mol^{-1}. The effect is attributed to interaction of mycorrhiza and potting mixture. In later phase (after 270 days of transplanting), when sandal seedlings had grown to a height of 18 to 20 cm they showed higher intercellular carbon dioxide concentration with pot host *A.sessilis*(290.85 µmol CO_2 mol^{-1}) and potting mixture sand , soil, vermicompost and *G.fasciculatum* (320.44 µmol CO_2 mol^{-1}) due to higher nutrient absorption because of microbial activity. AM fungi also helped in absorption and activation of phosphorous and potassium from rhizosphere through haustorial connection and there was lower intercellular concentration of $CO_2$with treatment of sand, soil and FYM (253.00 µmol CO_2 mol^{-1}) due to inability to support the seedlings through better absorption of nutrients. Lower intercellular concentration of carbon dioxide due to shading effect and lower leaf temperature was also observed during the experimentation. Collavino *et al.* (2016), according to whom concentrations of intercellular CO_2 control the opening of the stomata in relation to the photosynthetic demand of CO_2 in the plant.

Sandal seedlings which were grown using *C. junghuhiana* as a pot host or primary host recorded higher transpiration rate (1.39 mmol H_2O m^{-2} S^{-1}) and the seedlings with sub-treatment burnt rice husk, soil and FYM without AM fungi expressed higher transpiration rate (1.53 mmol H_2O m^{-2} S^{-1}). The result in case of transpiration rate falls in line with the observations for other physiological parameters. In this case, sandal seedlings grown with *C. junghuhniana* as a mycorrhizal host likely experienced enhanced nutrient and water uptake efficiency due to the symbiotic relationship with the mycorrhizal fungi. This improved nutrient and water uptake would lead to increased transpiration rates, as the plants are able to absorb and transport more water through their vascular system. On contrary, it was lowest for seedlings with sand, soil, vermicompost and *G.fasciculatum* (1.03 mmol H_2O m^{-2} S^{-1}) after 90 days of transplanting. However, after 270 days of transplanting, sandal seedlings with host *A.sessilis* exhibited higher transpiration (1.60 mmol H_2O m^{-2} S^{-1}) and the seedlings with treatment of sand, soil, FYM and*G. intraradices* (1.50 mmol H_2O m^{-2} S^{-1}). Higher transpiration rate in *A.sessilis* may be due to herb species which does not interfere with growth of sandals and higher entry of CO_2 into the mesophyll cells. As a result, the sandal seedlings may allocate more resources, including water, towards transpiration, leading to a higher transpiration rate.

Water use efficiency was found to be higher in seedlings grown with host plant *A. lebbeck*(2.05) and potting mixture sand, soil, FYM without AM fungi (2.34) and lesser with burnt rice husk, soil and FYM without AM fungi (1.07), after 90 days of transplanting. At the end of experiment, water use efficiency was maximum with pot host *C. junghuhniana*(2.62) and with treatment soil, sand and FYM without AM fungi (3.48). The water use efficiency is strongly related to temperature during the day, leaf temperature, relative humidity and CO_2 concentration. It is influenced by various factors such as precipitation, aridity levels, vapor pressure deficit (VPD), and soil moisture (Fatichi *et al.,* 2013).Additionally, plant water use theory has been developed within a plant-performance paradigm, but alternative hypotheses for drivers of water use and stomatal regulation exist, including using water to avoid thermal stress, promote reproduction, and hoard water.The present results are in line with studies by Shimazaki *et. al.* (2007) who opined that there is a close relationship between net photosynthesis and transpiration rate which implies that reductions in the net assimilation of CO_2 implies a lower loss of water by plants.Wolf (2016) further supports this, showing that plants may maximize carbon gain without pricing water loss, and that this behaviour is consistent with plant competition. This informationprovides a more comprehensive understanding of plant water use and stomatal regulation.

The carboxylation efficiency of sandal seedlings in different treatments and their interaction was very less even after 90 and 270 days of transplanting. The carboxylation efficiency was 0.01 in all the treatments imposed. However, it was 0.02 at the interaction of *C. junghuhiana* and sand, soil and FYM without AM fungi after 270 of transplanting. These results are in line with report by Sun *et al*. (2007) who opined that reduction of carboxylation efficiency is due to smaller amount of CO_2being fixed and non-stomatic factors which influenced the photosynthetic rate of the plants (Ferraz *et. al.,* 2012). Low temperatures cause a marked decrease in the photosynthetic rate, which is induced by biochemical limitations (Partelli, 2009). The low stomatal conductance and the corresponding low internal to ambient carbon dioxide concentration ratio have been reported to cause low photosynthetic rates resulting from low carboxylation and/or the mesophyll efficiency of CO_2 fixation capacity. In addition to the repression of several carboxylation enzymes, low temperatures are associated with a rapid breakdown of photosynthetic pigments, such as chlorophyll, causing a positive feedback loop, which further reduces the photosynthetic rates.Additionally, the imbalance in carbohydrate supply and demand, as well as the potential for direct inhibition of photosynthesis due to carbohydrate accumulation, could be contributing factors (Arp, 1991; Stitt, 1991).

In view of physiological development aspects, the sandalwood seedlings grown with pot host *Casuarina junghuhniana* had better physiological performance. Research consistently shows that the choice of host plant significantly impacts the physiological development of sandalwood seedlings. Balasubramanian (2021) found that sandalwood seedlings grown with leguminous hosts, such as *C. junghuhniana*, exhibited superior growth performance. This was further supported by Sahu (2021),who reported that sandalwood seedlings grown with *C. junghuhniana* had better height growth and collar diameter. The influence of the host plant on physiological attributes was also highlighted by Rocha (2014), who found that sandalwood trees growing with a host plant showed higher carbon assimilation, water absorption, and nutrient content which aligns with presents observations. Annapurna (2006) further emphasized the importance of the primary host in boosting the growth of sandalwood seedlings, with leguminous hosts being particularly beneficial. Hence the present study accentuates the critical role of the host plant, particularly leguminous hosts like *C. junghuhniana*, in enhancing the physiological performance of sandalwood seedlings.

The potting mixture combination, burnt rice husk, soil, FYM – in control and along with either AM strain (*Glomus fasiculatum* and *Glomus intraradices*) had an enhanced impact on physiological growth parameters as compared to other sub-treatments. The combination of burnt rice husk, soil, and FYM provides a nutrient-rich substrate for plant growth (Rajashekharand Geetha., 2017). FYM contributes organic matter and essential nutrients, while burnt rice husk enhances soil structure and nutrient retention. This nutrient-rich environment promotes vigorous root development and overall plant growth. Additionally, burnt rice husk and organic matter from FYM improve soil structure by increasing porosity and water retention capacity. This allows for better root penetration, aeration, and nutrient uptake, which are essential for optimal physiological growth. When combined with AM fungi such as *Glomus fasciculatum* and *Glomus intraradices*, it enhances microbial activity in the rhizosphere, promoting nutrient availability and plant growth (Mirjani *et al.*, 2019). The addition of AM fungi establishes a symbiotic relationship with plant roots, facilitating nutrient uptake, particularly phosphorus, and water absorption. This symbiosis improves plant health and vigour, leading to enhanced physiological growth parameters such as increased biomass, root/shoot ratio, and chlorophyll content. Healthy soil provides an optimal environment for plant growth and physiological development.

Conclusion

The cultivation of Indian sandalwood (*Santalum album* L.) presents a promising avenue for economic prosperity within the forestry sector, yet it faces challenges stemming from dwindling natural resources and environmental exigencies. The physiological attributes of sandalwood seedlings play a pivotal role in shaping their growth and development, with host plant varieties and potting mixtures enriched with mycorrhizae exerting significant influence.The present study, sheds light on the complex interactions between host plants, potting mixtures, and sandalwood seedling physiology. Results indicate that sandalwood seedlings exhibit varied physiological responses depending on their host plant and potting mixture composition. Host plants such as *Casuarina junghuhniana* demonstrate superior physiological performance, suggesting the importance of selecting appropriate host species for sandalwood cultivation. Furthermore, potting mixtures comprising burnt rice husk, soil, and FYM, especially in combination with mycorrhizae, show enhanced effects on sandalwood seedling physiology. These mixtures provide nutrient-rich substrates and promote microbial activity in the rhizosphere, facilitating nutrient uptake and water absorption. Overall, the study highlights the significance of adopting adaptive forest management strategies and improving cultivation practices to mitigate the challenges posed by climate change and dwindling natural resources. By understanding and optimizing sandalwood seedling physiology, stakeholders can pave the way for sustainable cultivation and ensure the continued prosperity of this invaluable botanical resource.

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Table A.1: Effect of host and potting mixture on CO_2 assimilation and stomatal conductance of sandal seedlings

Plot	**Treatment**	**CO_2 Assimilation rate (A)** (μmol CO_2 m^{-2} s^{-1})		**Stomatal conductance (gs)** (mol H_2O m^{-2} s^{-1})	
		90 DAP	**270 DAP**	**90 DAP**	**270 DAP**
Main plot (host)	**H1**	1.68	2.24	59.57	47.73
	H2	1.78	2.25	75.54	41.61
	H3	1.70	2.20	60.91	66.13
Sub plot treatment (Potting mixture)	**T1**	1.69	2.31	88.67	38.00
	T2	2.09	1.67	57.11	44.11
	T3	1.78	2.06	69.51	60.38
	T4	1.21	2.78	67.56	53.67
	T5	2.18	2.54	48.00	45.11
	T6	1.87	2.10	56.44	59.78
	T7	1.37	2.21	78.44	53.67
	T8	1.58	2.08	53.00	52.78
	T9	1.73	2.33	69.33	58.93
Interaction Effect (Host *potting mixture)	**H1*T1**	2.13	2.23	36.67	49.00
	H1*T2	1.77	1.93	40.00	50.00
	H1*T3	1.42	2.37	29.87	77.47
	H1*T4	0.67	2.73	90.67	31.00
	H1*T5	2.23	2.23	38.00	58.00
	H1*T6	1.90	2.00	31.13	54.13
	H1*T7	1.13	2.20	129.67	24.00
	H1*T8	1.63	1.77	60.67	39.00
	H1*T9	2.24	2.73	79.47	47.00
	H2*T1	1.13	3.07	86.33	32.67
	H2*T2	2.10	1.43	84.67	27.33
	H2*T3	2.16	2.27	91.80	29.53
	H2*T4	0.97	2.17	47.33	32.00
	H2*T5	1.87	2.20	41.67	34.33
	H2*T6	2.23	2.70	95.73	69.47
	H2*T7	1.57	2.20	77.33	48.33
	H2*T8	2.40	2.10	54.00	48.67
	H2*T9	1.59	2.13	101.00	52.13
	H3*T1	1.80	1.63	143.00	32.33
	H3*T2	2.40	1.63	46.67	55.00
	H3*T3	1.76	1.55	86.87	74.13
	H3*T4	2.00	3.43	64.67	98.00
	H3*T5	2.43	3.20	64.33	43.00
	H3*T6	1.48	1.60	42.47	55.73

	H3*T7	1.40	2.23	28.33	88.67
	H3*T8	0.70	2.37	44.33	70.67
	H3*T9	1.35	2.15	27.53	77.67

Table A.2: Effect of host and potting mixture on intercellular CO_2 concentration and transpiration rate of sandal seedlings

Plot	**Treatment**	**Intercellular CO_2 concentration (Ci)** (µmol CO_2 mol^{-1})		**Transpiration rate (E)** (mmol H_2O m^{-2} s^{-1})	
		90 DAP	**270 DAP**	**90 DAP**	**270 DAP**
Main plot (host)	**H1**	302.28	285.54	1.26	1.20
	H2	316.73	290.82	1.39	0.93
	H3	298.88	295.85	1.05	1.60
Sub plot treatment (Potting mixture)	**T1**	317.89	253.00	1.22	0.89
	T2	311.44	300.00	1.13	1.15
	T3	290.67	285.22	1.16	1.50
	T4	337.22	289.89	1.53	1.39
	T5	261.22	276.22	1.07	1.23
	T6	292.44	284.38	1.21	1.45
	T7	333.56	300.56	1.44	1.08
	T8	308.11	320.44	1.03	1.24
	T9	301.13	306.93	1.33	1.25
Interaction Effect (Host *potting mixture)	**H1*T1**	293.67	291.00	0.66	1.27
	H1*T2	283.33	285.67	0.85	1.32
	H1*T3	237.80	304.93	0.60	1.75
	H1*T4	330.67	214.67	1.91	0.99
	H1*T5	252.33	333.00	0.94	1.38
	H1*T6	244.27	248.27	0.77	1.35
	H1*T7	422.00	310.33	2.55	0.72
	H1*T8	342.33	311.67	1.30	0.97
	H1*T9	314.13	270.33	1.78	1.06
	H2*T1	345.67	217.33	1.51	0.56
	H2*T2	329.00	305.00	1.79	0.64
	H2*T3	347.20	257.27	1.84	0.72
	H2*T4	326.67	326.67	1.19	0.67
	H2*T5	279.33	271.00	0.99	0.94
	H2*T6	332.00	284.40	1.95	1.43
	H2*T7	294.67	308.67	1.05	1.03
	H2*T8	276.33	333.00	0.78	1.18
	H2*T9	319.73	314.07	1.43	1.19
	H3*T1	314.33	250.67	1.50	0.83
	H3*T2	322.00	309.33	0.76	1.47

	H3*T3	287.00	293.47	1.05	2.03
	H3*T4	354.33	328.33	1.47	2.53
	H3*T5	252.00	224.67	1.28	1.37
	H3*T6	301.07	320.47	0.90	1.57
	H3*T7	284.00	282.67	0.71	1.48
	H3*T8	305.67	316.67	1.01	1.58
	H3*T9	269.53	336.40	0.77	1.50

Table A. 3: Effect of host and potting mixture on water use efficiency and carboxylation efficiency of sandal seedlings

Plot	**Treatment**	**Water use efficiency**		**Carboxylation efficiency**	
		90 DAP	**270 DAP**	**90 DAP**	**270 DAP**
Main plot (host)	**H1**	2.05	2.39	0.01	0.01
	H2	1.75	2.62	0.01	0.01
	H3	1.84	1.92	0.01	0.01
Sub plot treatment (Potting mixture)	**T1**	2.34	3.48	0.01	0.01
	T2	2.19	1.70	0.01	0.01
	T3	2.41	1.93	0.01	0.01
	T4	1.07	2.67	0.00	0.01
	T5	2.10	2.64	0.01	0.01
	T6	1.74	1.67	0.01	0.01
	T7	1.56	3.23	0.01	0.01
	T8	2.15	1.54	0.01	0.01
	T9	1.35	1.90	0.01	0.01
Interaction Effect (Host *potting mixture)	**H1*T1**	4.53	2.27	0.01	0.01
	H1*T2	1.87	1.62	0.01	0.01
	H1*T3	3.04	1.42	0.01	0.01
	H1*T4	0.67	3.12	0.00	0.02
	H1*T5	2.47	1.55	0.01	0.01
	H1*T6	2.49	1.40	0.01	0.01
	H1*T7	0.49	5.87	0.00	0.01
	H1*T8	1.57	1.69	0.00	0.01
	H1*T9	1.30	2.54	0.01	0.01
	H2*T1	0.96	3.84	0.00	0.02
	H2*T2	1.37	1.99	0.01	0.00
	H2*T3	1.17	3.19	0.01	0.01
	H2*T4	1.61	3.42	0.00	0.01
	H2*T5	1.97	3.64	0.01	0.01
	H2*T6	1.21	2.65	0.01	0.01
	H2*T7	2.31	1.73	0.01	0.01
	H2*T8	3.90	1.44	0.01	0.01

	H2*T9	1.26	1.64	0.01	0.01
	H3*T1	1.53	4.32	0.01	0.01
	H3*T2	3.33	1.49	0.01	0.01
	H3*T3	3.02	1.19	0.01	0.01
	H3*T4	0.93	1.46	0.01	0.01
	H3*T5	1.84	2.74	0.01	0.01
	H3*T6	1.52	0.97	0.01	0.01
	H3*T7	1.88	2.09	0.01	0.01
	H3*T8	0.98	1.49	0.00	0.01
	H3*T9	1.49	1.52	0.01	0.01

Fig A.1: Physiological parameters measurements using Portable Photosynthesis System Meter (PPS Meter)

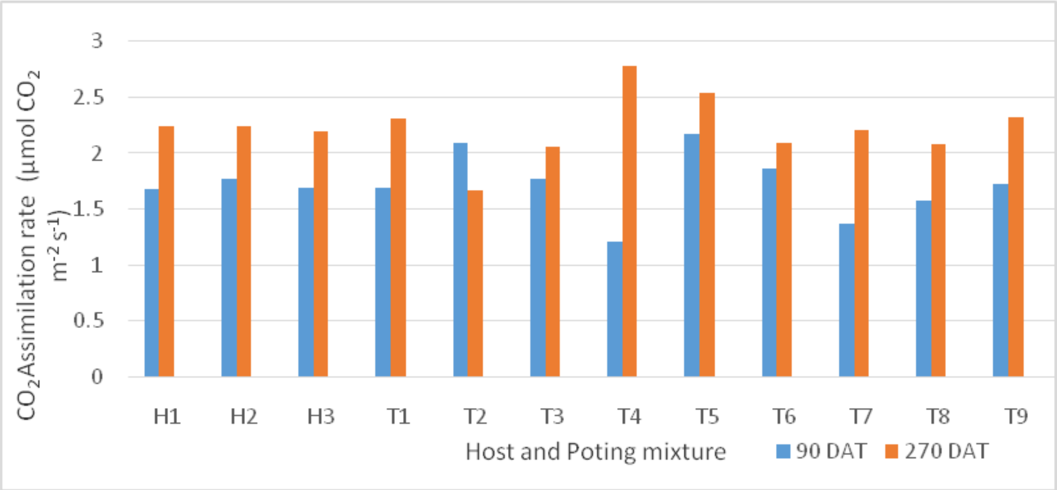

Fig. A.2: Effect of host and potting mixture on CO_2 Assimilation rate of sandal seedlings, after 90 and 270 days of transplanting

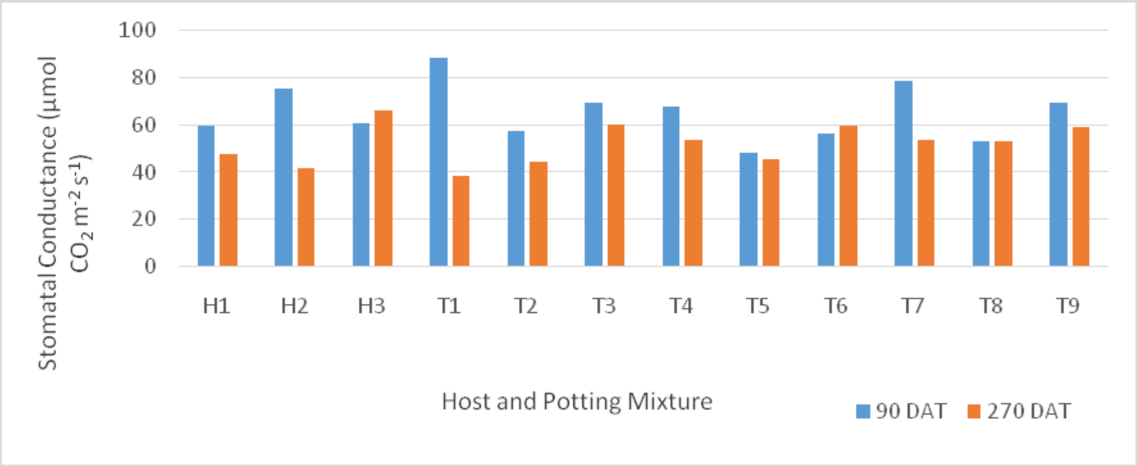

Fig A.3: Effect of host and potting mixture on Stomatal conductance of sandal seedlings, after 90 and 270 days of transplanting