

EFFECTS OF SOIL NUTRIENT AVAILABILITY ON ECTOMYCORRHIZAL COMMUNITIES' DISTRIBUTION IN TWO DIPTEROCARP SPECIES UNDER ELEVATED ATMOSPHERIC CARBON DIOXIDE

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The consequences of rising atmospheric carbon dioxide (CO₂) level on belowground communities in tropical rainforests continues to be a subject of debate. The main objective of this study was to investigate the distribution of ectomycorrhizal (ECM) fungi and relationship between soil nutrients availability under two different CO₂ concentrations. Free Air Carbon Dioxide Enrichment (FACE) hexagon plot was designed to monitor the impact of CO₂ in tropical rainforest ecosystems at Tekam Forest Reserve, Pahang, Malaysia. Twelve roots and soil samples were collected from two dipterocarp saplings (*Shorea lepidota* and *S. leprosula*) in both elevated CO₂ (FACE plot) and control plot conditions. Five soil properties: nitrogen (N), phosphorus (P), potassium (K), carbon (C), and the C:N ratio were analysed. In terms of species distribution, only four species of ECM were found in the FACE plot as opposed to five in the control plot. Unlike *Geastrum* sp. which was observed in the control plot, *Lactarius* sp., *Russula* sp., *Tomentella* sp., and *Cenococcum* sp. exist in both control and FACE plots, indicating their adaptability to varying soil nutrient and CO₂ conditions. Then the Detrended Correspondence Analysis (DCA), Principal Component Analysis (PCA), and Canonical Correspondence Analysis (CCA) were employed to establish the relationship between ECM fungi and their host plant, soil nutrient composition and host plant, and combining all parameters, respectively. *Shorea lepidota* displayed a tendency towards phosphorus in the control plot while *S. leprosula* showed a preference for higher carbon contents. *Tomentella* sp. and *Cenococcum* sp. showed strong association with nitrogen and potassium contents, respectively. Whilst, both *Lactarius* sp. and *Russula* sp. were highly associated with C:N ratio. Conclusively, our findings emphasize the need to understand the complex relationship between soil nutrient availability, ECM distribution and elevated atmospheric CO₂ in tropical rainforest ecosystems.

Keywords: Atmospheric CO₂, dipterocarpaceae, ECM fungi, soil nutrients

INTRODUCTION

Forest ecosystems are home to a diverse range of organisms, including the valuable players known as ectomycorrhizal fungi (ECM), which form beneficial connections with many plant species. They form associations with approximately 60% of plant stems on Earth (Steidinger et al. 2019) and provide host plants with approximately 80% of their annual nitrogen requirements (Leake et al. 2004). These root-symbionts are prolific hyphae producers and significantly enhance the soil volume explored by fine roots (Smith & Read 2010). They constitute over 30% of the soil microbial biomass in boreal and temperate forest ecosystems (Högberg & Högberg 2002).

The establishment and maintenance of ECM symbiosis are influenced by various factors such as the unique traits of plants studied by Bauman *et al.* (2016), Chot and Reddy (2022), López-García *et al.* (2017) and Shi *et al.* (2023), and the intriguing exudate profiles investigated by Soudzilovskaia *et al.* (2015) and Wong-Bajracharya *et al.* (2020). Additionally, researchers like Veach *et al.* (2018) have shed light on the importance of resource allocation in these mutually beneficial relationships.

The primary benefits of ECM fungi to the host plant are an increased range for the uptake of nutrients such as phosphorus (P) and nitrogen (N), as well as increase in drought and disease resistance (Augé 2001, Domínguez-Núñez *et al.* 2019, Hagenbo *et al.* 2020, Lehto & Zwiazek 2011, Smith & Read 2010). In return, the fungi received carbon (C) in the form of photosynthate. The establishment and functioning of such symbioses are influenced by various factors including photosynthetic rates (Gardner *et al.* 2021), carbon allocation (Naing *et al.* 2016, Pan *et al.* 2020), and modifications in root exudates composition (Bardgett *et al.* 2014, Bernard *et al.* 2022, Finzi *et al.* 2015, Huang *et al.* 2014).

Among these factors, the concentration of CO₂ in the atmosphere has emerged as a key driver that shapes plant-soil interactions and belowground communities. Elevated CO₂ levels not only affect aboveground vegetation but also induce notable changes in plant physiology (Bhargava & Mitra 2020), morphology (Barickman *et al.* 2021, Luo *et al.* 2020), growth patterns (Brito *et al.* 2020, Piñero *et al.* 2017), and root architecture (Ziegler *et al.* 2023). Consequently, the intricate connections between plants and the belowground environment, particularly ECM fungi, are significantly influenced by elevated CO₂ concentrations.

Increased atmospheric CO₂ not only affects the plant but also has profound impacts on the physical and chemical properties of the soil. Changes in CO₂ levels can influence soil moisture (Burkart *et al.* 2011, Lemordant *et al.* 2018), nutrient availability (Madhu & Hatfield 2013, Wong-Bajracharya *et al.* 2020), soil carbon stocks (Terrer *et al.* 2021, Walker *et al.* 2021), organic matter decomposition rates (Li *et al.* 2023) and nutrient cycling processes (Jiang *et al.* 2020a, Liu *et al.* 2018). These modifications

in soil properties form a dynamic feedback loop that further influences plant responses and the availability of resources for ECM fungi (Daza *et al.* 2005, Zak *et al.* 2019).

Currently, little is known about the actual relationships and the real interplay between changes in plant communities and the properties of the soil under different climates. Further, as the colonisation dynamics, diversity and functioning of ECM fungi are intricately linked to the quality and quantity of resources they can access in soil, this study aimed to investigate the relationship between soil nutrient availability and the distribution of ectomycorrhizal (ECM) fungi under two different CO₂ concentrations (0 and 100–300 ppm). By examining the responses of ECM fungi to changing CO₂ levels, adaptations and shifts in plant-microbe interactions that may occur in future high-CO₂ environments can be predicted.

MATERIALS AND METHODS

Study site

The study was conducted within the Tekam Forest Reserve in Jerantut, Pahang, a hill dipterocarp forest characterised by its diverse soil composition. The soil in this area predominantly consists of pyroclastic and volcanic rocks, evident by historical volcanic activity (Khoo 1977, Marryanna *et al.* 2019). The soil texture ranges from clay (42%) to sandy (37%) (Amir Husni *et al.* 1989) providing a varied substrate for plant growth and nutrient dynamics. Tekam Forest Reserve experiences a bimodal rainfall pattern, with peaks in precipitation occurring in November and May (Marryanna *et al.* 2019). The average annual precipitation in the study area is approximately 2987 mm (Weather and Climate 2022).

Free Air Carbon Enrichment (FACE) plot description

Within the Tekam Forest Reserve, the FACE system was implemented to investigate the effect of elevated atmospheric CO₂ levels on the forest ecosystems. The FACE system was hexagonally designed with a side length of 6.0 m on each side. Functioning as an open-chamber plot, CO₂ gas is released into the experimental area

at desired levels (100–300 ppm) within 24 hours (Norsheilla et al. 2018). These concentrations were chosen to mimic the high levels of atmospheric CO₂ concentrations under natural field conditions. The system was also designed to maintain air temperature and humidity while the CO₂ concentration was elevated above normal levels. To ensure accurate reading of selected parameters, the FACE system is integrated with a control panel house and computerised data monitoring, providing real-time insights into the environmental conditions and CO₂ levels within the experimental plot.

Ectomycorrhizal (ECM) diversity identification

The roots of three selected saplings of both *Shorea lepidota* and *S. leprosula* in both conditions (control and FACE plot) were meticulously traced and excised using a sharp knife. To minimise damage to infected roots, the samples were gently submerged in water, allowing for the careful removal of excess soil and debris before transferring to a clean petri dish containing water. The ECM morphotypes were then identified under a dissecting microscope, based on criteria such as shape, dimensions, surface features, ramification type, colour, size, and the presence of emanating hyphae, rhizomorphs, and cystidia (Agerer & Rambold 2004–2020). Morphotypes exhibiting similar morphological characteristics were pooled and quantified accordingly. Identification and verification of the anatomical and morphological features of ECM structures were conducted using standard ECM descriptions from reference books (Agerer 1987–2006) and the DEEMY online database (Agerer & Rambold 2004–2020).

Soil sampling

A total of 12 soil samples were collected from the bases of three replicates of dipterocarp (*S. lepidota* and *S. leprosula*) saplings at two different plots. Prior to soil sampling, any leaf litter and humus layers were carefully removed. Both *S. lepidota* and *S. leprosula* saplings were chosen as they are commonly found in lowland dipterocarp forests and fast-growing species (Manokaran et al. 1992, Masano et al. 1987, Widiyatno et al. 2014). To avoid the influence of

plant size, the selection of plant saplings with a similar range of height (average of 0.32 m) was random among dipterocarp saplings. Topsoil samples from 0–20 cm depth were collected for each species and carefully placed in polybags and air dried. Subsequent analysis of the soil nutrients availability- nitrogen (N), phosphorus (P), potassium (K), carbon (C), and the C:N ratio was done according to Nurul Hidayah et al. (2020).

Analysis of ECM communities and soil properties under different CO₂

The relationship between ECM communities and soil properties was analysed using Canoco 5.0 software (Biometrics, Wageningen, The Netherlands). Detrended Correspondence Analysis (DCA) was first performed to visualise the similarity of ECM species to host species in two plots. The control plot represents normal (0 ppm) while the FACE plot represents elevated CO₂ levels (100–300 ppm). Binary transformation was used to standardise the relative abundance of ECM species. Unconstrained Principal Component Analysis (PCA) was carried out next to identify the variation in soil properties and the distribution of host plants in relation to soil nutrients. The chosen gradient length of DCA was 3.45 indicating that the data were appropriate for conducting Canonical Correspondence Analysis (CCA) (Ter Braak 1986). The CCA allowed for visualisation of sites and species in multidimensional spaces, with the restriction that the ordination axes must be linear combinations of the specified underlying soil nutrients. The significance of each soil variable was determined through a Monte Carlo permutation test based on 499 random trials at a significance level of 0.05 (Ter Braak 1990).

RESULTS AND DISCUSSION

ECM composition

Table 1 presents the occurrence of ectomycorrhizal (ECM) fungi families and genera associated with *S. lepidota* and *S. leprosula* saplings in both control and FACE (Free-Air CO₂ Enrichment) plots. The ECM families considered in this study include Theleporaceae, Geastraceae, Gloniaceae and Russulaceae represented by the

Table 1 Ectomycorrhizal (ECM) occurrence on two host plant species (*Shorea lepidota*, *S. leprosula*) under two different conditions (control and FACE plots)

Condition	Host plant	Theleporaceae	Geastraceae	Gloniaceae	Russulaceae	
		<i>Tomentella</i>	<i>Geastrum</i>	<i>Cenococcum</i>	<i>Russula</i>	<i>Lactarius</i>
Control plot	<i>S. lepidota</i>	✓	✓	✓	✓	✓
	<i>S. leprosula</i>	✓	✓	✗	✓	✓
FACE plot	<i>S. lepidota</i>	✓	✗	✗	✓	✓
	<i>S. leprosula</i>	✓	✗	✓	✗	✓

genera *Tomentella*, *Geastrum*, *Cenococcum*, *Russula* and *Lactarius*. In the control plot, *S. lepidota* exhibited associations with all the ECM genera listed (*Tomentella*, *Geastrum*, *Cenococcum*, *Russula* and *Lactarius*), suggesting a rich and diverse ECM community under normal conditions. In contrast, *S. leprosula* showed associations with most of the genera except *Cenococcum*, indicating slightly reduced ECM diversity compared to *S. lepidota*. Under elevated CO₂ conditions (FACE plot), the ECM diversity associated with *S. lepidota* decreased together with the absence of both *Geastrum* and *Cenococcum*, indicating a potential sensitivity of these genera to elevated CO₂ levels. On the other hand, *Tomentella*, *Russula* and *Lactarius* persisted, suggesting that these genera are more resilient or adaptable to elevated CO₂ conditions, consistent with studies done by Fransson et al. (2005) and Lindahl et al. (2006). *Shorea leprosula* in the FACE plot showed a similar trend, with the absence of *Geastrum* and *Russula*. However, *Cenococcum* reappeared in the FACE plot for *S. leprosula*, suggesting possible compensatory colonisation by *Cenococcum* under elevated CO₂ conditions while *Russula* remained absent (Pritchard et al. 2008).

The differing responses of *S. lepidota* and *S. leprosula* to elevated CO₂ in terms of ECM associations suggest species-specific interactions between host plants and their mycorrhizal partners. For instance, *S. lepidota* showed a broader ECM diversity under the control conditions but a more pronounced reduction in diversity under elevated CO₂, whereas *S. leprosula* maintained some level of ECM diversity even in the FACE plot, with *Cenococcum* reappearing. This could indicate that *S. leprosula* has a more flexible or resilient ECM association, possibly aiding its adaptability under changing

environmental conditions (Van Der Putten et al. 2013, Parrent & Vilgalys 2007).

These findings align with the research of Norby et al. (2010) who reported species-specific responses in ECM diversity under elevated CO₂ in temperate forests, suggesting that different host plants may exhibit varied mycorrhizal associations depending on environmental conditions. Similarly, Parrent and Vilgalys (2007) found that ECM fungal communities are strongly influenced by host plant identity, which is consistent with the observed differences in ECM associations between *S. lepidota* and *S. leprosula* in this study. A previous study recorded increases in ECM abundance under elevated CO₂ (Treseder 2004). However, findings from this study revealed a reduction in ECM diversity, particularly for *S. lepidota*, suggesting that tropical ECM communities may respond differently with some genera potentially more sensitive to elevated CO₂ levels. The observed changes in ECM community structure could have significant implications for nutrient acquisition, as different ECM fungi are known to vary in their efficiency of nutrient uptake, particularly in acquiring P and N from the soil (Agerer 2001, Courty et al. 2010). The persistence of *Tomentella* and *Lactarius* in both conditions suggested that these genera might play a crucial role in maintaining nutrient cycling and supporting plant growth, despite the overall reduction in diversity. Courty et al. (2010) reported that *Lactarius* spp. appear under elevated CO₂, possibly due to its efficient nutrient uptake capabilities. Interestingly, their study also showed that *Geastrum* spp. were observed to have declined under elevated CO₂, potentially due to its specific ecological preferences or host requirements (Högberg et al. 2007, Peay et al. 2010).

Table 2 Summary of soil nutrients at Tekam Forest Reserve, Jerantut, Pahang

Nutrient	Control plot	FACE plot	Combination
N (%)	0.37	0.43	0.40
P (mg kg ⁻¹)	4.20	3.33	3.77
K (mg kg ⁻¹)	84.93	81.78	83
C (%)	1.49	1.69	1.59
C:N (%)	4.38	4.93	4.66

Soil nutrient availability

Understanding variations in soil nutrient content is crucial for comprehending plant nutrient acquisition strategies and their responses to elevated CO₂ levels. This study assessed primary macronutrients (N, P, K) essential for plant growth, along with carbon (C) content and the C:N ratio, which are important indicators of nutrient availability and decomposition processes (Blanco et al. 2023, Ostrowska & Porebska 2015, Zhang et al. 2019, Zheng et al. 2021) (Table 2).

The results revealed minor variations in soil nutrient content between control and FACE plots. Nitrogen (N) content was slightly higher in the FACE plot (0.43%) compared to the control plot (0.37%). Phosphorus (P) and potassium (K) levels were slightly lower in the FACE plot (3.33 mg kg⁻¹ and 81.78 mg kg⁻¹, respectively) compared to the control plot (4.20 mg kg⁻¹ and 84.93 mg kg⁻¹). Carbon content was higher in the FACE plot (1.69%) compared to the control plot (1.49%). The C:N ratio was higher in the FACE plot (4.93) compared to the control plot (4.38). The two-sample t-test indicated no significant difference in soil nutrient content between the two plots [$t(7) = 0.03$, p -value = 0.978].

Our finding suggests that elevated CO₂ levels have minimal impact on soil nutrient dynamics in the short term, consistent with similar studies in tropical forests (Zheng et al. 2021). The minimal variation in soil nutrient content implies that the tropical forest ecosystem may exhibit high resilience to changes in atmospheric CO₂, potentially due to complex interactions among soil microorganisms, plant roots, and broader ecosystem processes (Hungate et al. 1997, Luo et

al. 2006). This stability could also reflect the role of unmeasured factors such as microbial activity and root exudates, in maintaining nutrient balance under elevated CO₂ (Schlesinger et al. 2006, Drake et al. 2011).

Moreover, while elevated CO₂ can enhance plant growth and carbon sequestration, its impact on soil nutrient cycling can be limited or negligible in the short term, especially in nutrient-rich tropical ecosystems (Norby et al. 2011). This aligns with the observed minimal changes in nutrient content and supports the notion that tropical forest soils might buffer against atmospheric changes, maintaining nutrient dynamics even under altered environmental conditions (Thompson et al. 2019, Oren et al. 2001).

Relationship of ECM with host species and soil nutrient at different environments

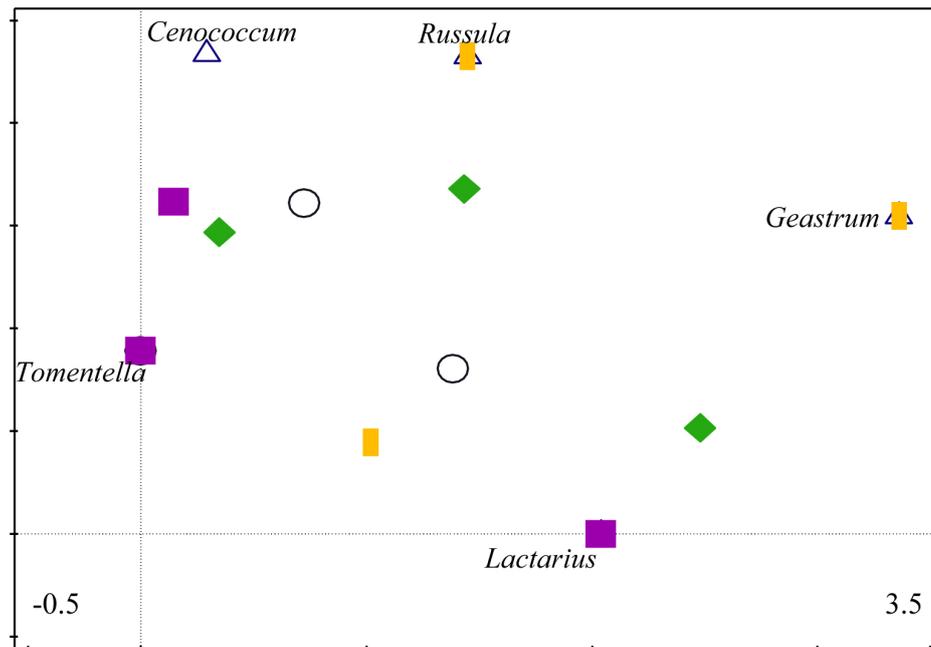
Detrended Correspondence Analysis (DCA)

DCA was employed to examine the relationship between ectomycorrhizal (ECM) fungi and their host plants, specifically *S. lepidota* and *S. leprosula*, in different CO₂ environments. The results of the DCA are summarised in Table 3, which includes eigenvalues and the cumulative explained variation for each axis. Axis 1, with an eigenvalue of 0.59, explained 41.29% of the cumulative variation in shaping the ECM community. The gradient length for Axis 1 was 3.18, reflecting significant separation of ECM species and host plants along this axis.

Under control conditions, DCA revealed a strong association between *S. leprosula* and the ECM fungi *Geastrum* sp. and *Russula* sp. (Figure 1). This suggests that under normal CO₂ levels, *S.*

Table 3 Summary of Detrended Correspondence Analysis (DCA) on ectomycorrhizal (ECM) community in Tekam Forest Reserve

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.5933	0.2735	0.013	0.0018
Explained variation (cumulative)	41.29	60.32	61.23	61.35
Gradient length	3.18	2.27	2.23	2.45

**Figure 1** Detrended Correspondence Analysis (DCA) of five ECM with 12 soil samples in Tekam Forest Reserve. For control plot, *Shorea leprosula* is coded in rectangular (yellow) while *S. lepidota* in diamond (green). For FACE plot, *S. leprosula* is coded in square (purple) while *S. lepidota* in empty circle (black)

leprosula establishes good symbiotic relationship with these specific ECM genera, which may optimise nutrient acquisition strategies under current environmental conditions (Courty et al. 2010). In contrast, under elevated CO₂ conditions (FACE plot), *S. leprosula* showed a shift in associations, favouring *Lactarius* sp. and *Tomentella* sp. over *Geastrum* sp. and *Russula* sp. This shift may reflect changes in root exudate composition or physiological responses of *S. leprosula* to elevated CO₂, which in turn altered the ECM community structure (Treseder 2004, Van der Putten et al. 2013).

Shorea lepidota exhibited weaker or minimal associations with ECM fungi in both control and FACE plots, suggesting that it may not rely as heavily on ECM symbiosis as *S. leprosula*, or

it may associate with ECM fungi not captured in this analysis. This could indicate that *S. lepidota* has a more stable but less diverse ECM community or is less responsive to CO₂-induced changes (Parrent & Vilgalys 2007). The observed limited associations of *Cenococcum* sp., known for its stress tolerance and ability to thrive in various environments, with both *S. leprosula* and *S. lepidota* may suggest that *Cenococcum* operates more independently or in a generalist role, rather than forming specific associations with these host plants (Agerer 2001, Courty et al. 2010).

The findings indicate that variations in ECM fungal associations are more likely driven by host specificity rather than soil nutrient status. The DCA analysis demonstrated distinct ECM-

Table 4 Summary of Principal Component Analysis (PCA) on the plant host in study plots in the Tekam Forest Reserve Jerantut, Pahang

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.5067	0.2972	0.1583	0.0378
Explained variation (cumulative)	50.67	80.39	96.22	100.00

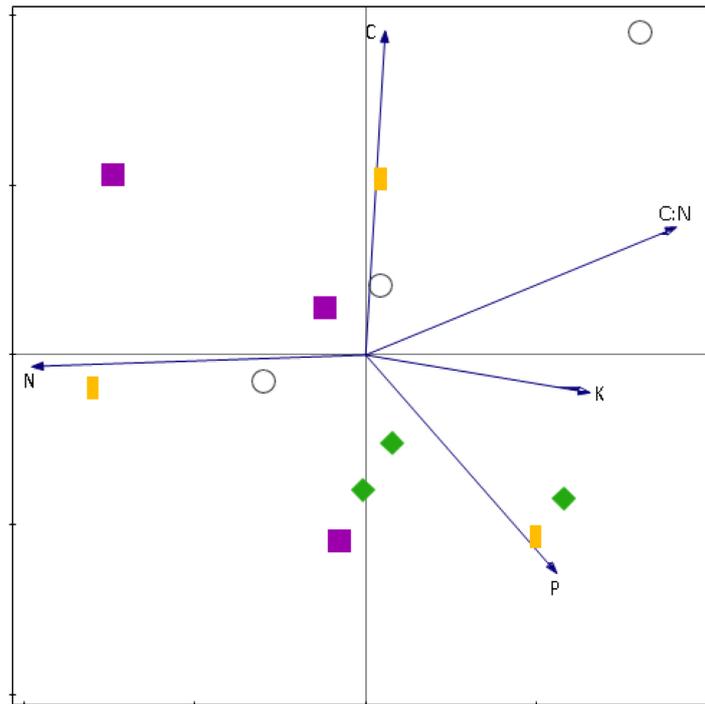


Figure 2 The Principal Correspondence Analysis (PCA) of 12 soil samples in Tekam Forest Reserve (P=available phosphorus; K=available potassium; N= total nitrogen, C= total carbon, C:N=ratio of total carbon and nitrogen). For control plot, *Shorea leprosula* is coded in rectangular (yellow) while *S. lepidota* in diamond (green). For FACE plot, *S. leprosula* is coded in square (purple) while *S. lepidota* in empty circle (black)

host plant associations that change under different environmental conditions (control vs. FACE plots) but remain consistent within each host plant species. This suggests that ECM fungi select their hosts based on specific plant characteristics such as root exudates, rather than soil nutrient availability alone (Parrent & Vilgalys 2007, Smith & Read 2010). The minimal variation in soil nutrient content between control and FACE plots (Table 2) supports this notion, indicating that nutrient status does not solely drive differences in ECM community structure. The stability in nutrient content across conditions suggests that other factors such as host plant-specific interactions with fungi, are more influential (Treseder 2004).

Principal Component Analysis (PCA)

The variations of soil nutrients of these samplings were investigated using PCA and summarised in Table 4. PCA was performed to analyse the relationship between plant host and the soil nutrients availability. The first two PCA eigenvalue axes had values of 0.507 and 0.297, explaining 50.67% and 80.39% of the variance, respectively. These showed significant relationships between soil nutrients with both axes, and that the distribution of the plant hosts is strongly controlled by soil nutrients in general. Figure 2 illustrated that nitrogen (N) and carbon (C) are closely associated with plant hosts in both control and FACE plots. In contrast, phosphorus

Table 5 Summary of Canonical Correspondence Analysis (CCA) on the ECM community in study plots in the Tekam Forest Reserve, Jerantut, Pahang

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.2949	0.1996	0.0363	0.0012
Explained variation (cumulative)	20.52	34.41	36.93	37.01
Pseudo-canonical correlation	0.8073	0.7393	0.3128	0.0686
Explained fitted variation (cumulative)	55.44	92.96	99.78	100.00

(P) shows a strong association only in the control plot, while potassium (K) and the C:N ratio do not significantly influence plant distribution. The PCA results indicate that soil nutrient levels directly influence host plant distributions. This means that variations in soil nutrients can affect where different host plants are found. However, the analysis does not explicitly address how soil nutrients might influence ECM fungi distribution via plant hosts.

Our findings suggest that soil nutrients play a key role in shaping host plant distributions, which may in turn, affect ECM fungi indirectly. While the PCA results show direct associations between soil nutrients and plant hosts, the indirect effects on ECM fungi distribution should be considered in the context of host plant changes. Previous studies have reported inconsistent results regarding the impact of soil nutrients on ECM colonisation, with some showing positive effects (Terrer et al. 2016, Wang et al. 2015) and others reporting negative effects (Alberston et al. 2007, Hu et al. 2006). In tropical rainforests, elevated CO₂ can affect ECM fungi colonisation by altering plant community dynamics and nutrient availability (Ellsworth et al. 2017, Jiang et al. 2020b). The intermediate-host plant stress hypothesis suggests that ECM communities are typically higher under moderate stress levels but may decrease under severe stress (Swaty et al. 2004). Although our results did not show statistically significant changes in ECM fungi distribution, the lower soil moisture observed in the FACE plot could contribute to reduced ECM colonisation, as adequate water availability supports a higher diversity of ECM fungi by providing increased carbohydrates to the underground community (Gehring et al. 2014).

Canonical Correspondence Analysis (CCA)

The CCA was used to explore relationships between soil nutrients and ECM communities in the Tekam Forest Reserve. As detailed in Table 5, CCA Axis 4 explained 37.0% of the variation in ECM community distribution, with a pseudo-canonical correlation of 0.81. However, the Monte Carlo permutation test showed no significant correlations across the axes (pseudo-F=1.0, p=0.40), indicating that the influence of soil nutrients on ECM community distribution was minimal. The CCA results illustrated the interactions between specific soil elements and ECM communities, as shown in Figure 3. For instance, *Russula* sp. and *Lactarius* sp. were associated with an enriched C:N ratio, suggesting their preference for nutrient conditions prevalent in specific environments. In the control plot, *S. leprosula* exhibited notable associations with certain ECM fungi. Whereas in the FACE plot, *S. lepidota* demonstrated different fungal associations. Notably, *Tomentella* sp., known for its preference for nitrogen-rich soils, was more commonly associated with *S. lepidota* in the control plot. Interestingly, our analysis revealed that neither potassium nor the C:N ratio had a significant impact on plant species distribution in either plot.

This finding contrasts with studies conducted in temperate forests, which found a strong preference for high C:N ratios by ECM fungi (Averill et al. 2014, Lin et al. 2017). In tropical rainforests, the influence of soil nutrients on ECM community distribution appears to be less pronounced, possibly due to the complex nature of nutrient-fungal interactions and the ability of fungi to utilise

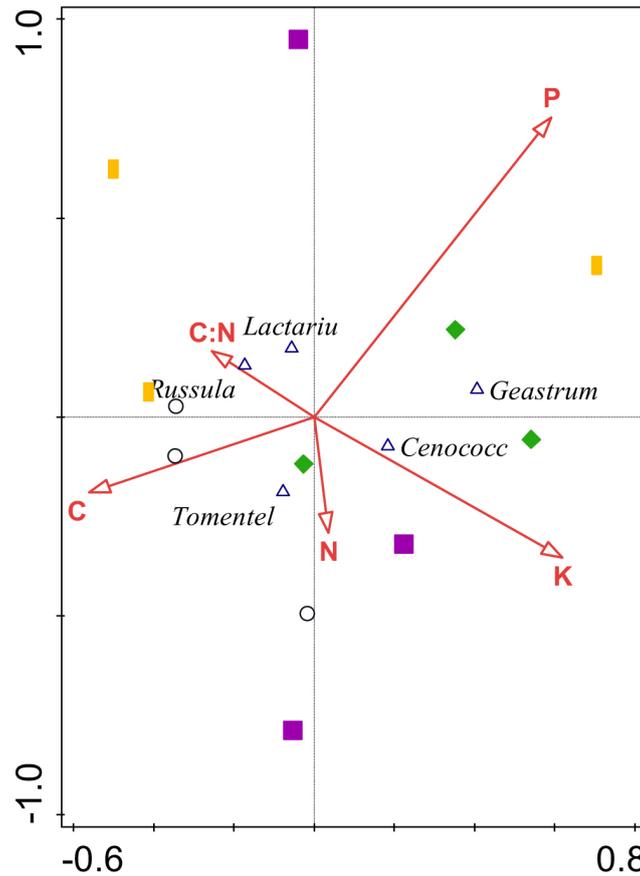


Figure 3 Canonical Correspondence Analysis (CCA) ordination plot showing the relationships among ECM fungi species, host plants, and soil nutrient availability under ambient (control) and elevated CO₂ (FACE) conditions. Length and direction of vectors indicate the strength and direction of the influence of soil nutrients (P = available phosphorus; K = available potassium; N = total nitrogen; C = total carbon; C:N= carbon to nitrogen ratio) on both ECM fungi and host plant species. For control plot, *Shorea leprosula* is represented by yellow rectangles and *S. lepidota* by green diamonds. For FACE plot, *S. leprosula* is represented by purple squares and *S. lepidota* by black empty circles

available nutrients efficiently (Abuzinadah & Read 1986). Soil nutrients play a crucial role in ECM fungi colonisation, as ECM fungi are essential for nitrogen cycling by decomposing organic complexes (Avis et al. 2003, Twieg et al. 2009). For instance, *Tomentella* sp. is known for its role in nitrogen uptake, aligning with its classification as a nitrophile (Hagenbo et al. 2018, Jörgensen et al. 2022, Ning et al. 2018, Sterkenburg et al. 2015). Phosphorus storage and transport are also vital, with ECM fungi facilitating favourable conditions for nutrient cycling (Casieri et al. 2013, Costa et al. 2016, Nehls & Plassard 2018, Van Tichelen & Colpaert 2000). Previous research indicated that Dipterocarpaceae species have strong associations with specific soil nutrients, particularly phosphorus, magnesium, and

calcium (Paoli et al. 2005). Other soil characteristics, including exchangeable calcium, magnesium and potassium, influence dipterocarp community composition in Borneo forests (Sukri et al. 2012). These findings underscore the complexity of nutrient-fungal interactions in tropical rainforests and suggest that ECM community structure may be influenced by factors beyond soil nutrient availability alone. In summary, while our CCA results did not reveal statistically significant correlations, they provide valuable insights into the nuanced interactions between soil nutrients and ECM communities. The minimal impact of soil nutrients observed in our study highlights the need for further research to understand the broader ecological factors influencing ECM fungal distribution in tropical ecosystems.

CONCLUSION

This study examined the relationship between soil nutrients and the distribution of ECM fungi under normal (control plot) and elevated CO₂ concentrations (FACE plot). Our findings indicate that elevated CO₂ concentrations lead to specific changes in the associations between Dipterocarpaceae plants and their environment, specifically impacting the connection between host plants and ECM fungi communities. Nitrogen availability had a more pronounced effect on ECM fungi distribution compared to phosphorus. Elevated CO₂ levels significantly influence soil nutrient availability and mycorrhizal community composition, as noted in recent studies (Tarin et al. 2021, Zhang et al. 2016). Additionally, increased atmospheric CO₂ can raise total carbon levels, potentially leading to soil acidification and affecting microbial communities. For instance, Wang et al. (2022) observed decreased basidiomycota abundance due to increased soil acidification from high organic carbon. Therefore, further research is needed on how soil nutrients affect ECM fungi diversity associated with Dipterocarpaceae in tropical forests. Our results support predictions that elevated CO₂ promotes plant growth and carbon sequestration, with subsequent effects on soil carbon levels (Wang et al. 2019, Chen et al. 2020). Understanding these impacts is crucial for forest ecosystem research, highlighting the need for ongoing investigation into how soil nutrients drive ECM fungi assembly under changing atmospheric conditions.

REFERENCES

- ABUZINADAH RA & READ DJ. 1986. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. III. Protein utilisation by *Betula*, *Picea* and *Pinus* in mycorrhizal association with *Hebeloma crustuliniforme*. *New Phytologist* 103: 507–514. <https://doi.org/10.1111/j.1469-8137.1986.tb02886.x>.
- AGERER R. & RAMBOLD G. 2004–2020. DEEMY — An information system for characterisation and determination of ectomycorrhizae. München, Germany.
- AGERER R. 1987–2006. Colour atlas of ectomycorrhizae: 1st–13th delivery. Einhorn-Verlag, Schwäbisch Gmünd.
- AGERER R. 2001. Exploration types of ectomycorrhizae. *Mycorrhiza* 11: 107–114. <https://doi.org/10.1007/s005720100108>.
- ALBERTON O, KUYPER TW & GORISSEN A. 2007. Competition for nitrogen between *Pinus sylvestris* and ectomycorrhizal fungi generates potential for negative feedback under elevated CO₂. *Plant and Soil* 296: 159–172. <https://doi.org/10.1007/s11104-007-9306-5>.
- AMIR HUSNI MS, MONA Z, MOHD GHAZALI H & ROZITA A. 1989. Nutrient Dynamics of Tekam Forest Reserve, Peninsular Malaysia, Under Different Logging Phases. *Journal of Tropical Forest Science* 2: 71–80.
- AUGÉ RM. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11: 3–42. <https://doi.org/10.1007/s005720100097>.
- AVERILL C, TURNER BL & FINZI AC. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* 505: 543–545. <https://doi.org/10.1038/nature12901>.
- AVIS PG, MCLAUGHLIN DJ, DENTINGER BC & REICH PB. 2003. Long-term increase in nitrogen supply alters above- and below-ground ectomycorrhizal communities and increases the dominance of *Russula* spp. in a temperate oak savanna. *New Phytologist* 160: 239e253. <https://doi.org/10.1046/j.1469-8137.2003.00865.x>
- BARDGETT RD, MOMMER L & DE VRIES FT. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology and Evolution* 29: 692–699. <https://doi.org/10.1016/j.tree.2014.10.006>.
- BARICKMAN TC, OLORUNWA OJ, SEHGAL A, WALNE CH, REDDY KR & GAO W. 2021. Interactive Impacts of Temperature and Elevated CO₂ on Basil (*Ocimum basilicum* L.) Root and Shoot Morphology and Growth. *Horticulturae* 7: 112. <https://doi.org/10.3390/horticulturae7050112>.
- BAUMAN D, RASPÉ O, MEERTS P, DEGREEF J, ILUNGA MULEDI J & DROUET T. 2016. Multiscale assemblage of an ectomycorrhizal fungal community: the influence of host functional traits and soil properties in a 10-ha miombo forest. *FEMS Microbiology Ecology* 92: fiw151. <https://doi.org/10.1093/femsec/fiw151>.
- BERNARD L, BASILE-DOELSCH I, DERRIEN D ET AL. 2022. Advancing the mechanistic understanding of the priming effect on soil organic matter mineralization. *Functional Ecology* 36: 1355–1377. <https://doi.org/10.1111/1365-2435.14038>.
- BHARGAVA S & MITRA S. 2020. Elevated atmospheric CO₂ and the future of crop plants. *Plant Breeding* 140: 1–11. <https://doi.org/10.1111/pbr.12871>.
- BLANCO JA, DURÁN M, LUQUIN J, SAN EMETERIO L, YESTE A & CANALS RM. 2023. Soil C/N ratios cause opposing effects in forests compared to grasslands on decomposition rates and stabilization factors in southern European ecosystems. *Science of Total Environment* 888: 164118. <https://doi.org/10.1016/j.scitotenv.2023.164118>.
- BRITO FAL, PIMENTA TM, HENSCHEL JM, MARTINS SCV, ZSÖGÖN A & RIBEIRO DM. 2020. Elevated CO₂ improves assimilation rate and growth of tomato plants under progressively higher soil salinity by decreasing abscisic acid and ethylene levels. *Environmental and Experimental Botany* 176: 104050. <https://doi.org/10.1016/j.envexpbot.2020.104050>.

- BURKART S, MANDERSCHIED R, WITTICH KP, LOEPMEIER Fj & WEIGEL HJ. 2011. Elevated CO₂ effects on canopy and soil water flux parameters measured using a large chamber in crops grown with free-air CO₂ enrichment. *Plant Biology* 13: 258–69. <https://doi.org/10.1111/j.1438-8677.2010.00360.x>.
- CASIERI L, NASSIMA AL, DOIDY J ET AL. 2013. Biotrophic transportome in mutualistic plant-fungal interactions. *Mycorrhiza* 23: 597–625. <https://doi.org/10.1007/s00572-013-0496-9>.
- CHEN Y, SUN R, SUN T, CHEN P, YU Z & DING L. 2020. Evidence for involvement of keystone fungal taxa in organic phosphorus mineralization in subtropical soil and the impact of labile carbon. *Soil Biology and Biochemistry* 148: 107900.
- CHOT E & REDDY MS. 2022. Role of Ectomycorrhizal Symbiosis Behind the Host Plants Ameliorated Tolerance Against Heavy Metal Stress. *Frontiers Microbiology* 13: 855473. <https://doi.org/10.3389/fmicb.2022.855473>.
- COSTA M, GAMA-RODRIGUES A, GONÇALVES J, GAMA-RODRIGUES E, SALES M & ALEIXO S. 2016. Labile and non-labile fractions of phosphorus and its transformations in soil under *Eucalyptus* plantations. *Brazil Forests* 7: 15. <https://doi.org/10.3390/f7010015>.
- COURTY PE, BUÉE M, DIEDHIOU AG ET AL. 2010. The role of ectomycorrhizal communities in forest ecosystem processes: New perspectives and emerging concepts. *Soil Biology and Biochemistry* 42: 679–698. <https://doi.org/10.1016/j.soilbio.2009.12.00>.
- DAZA A, MANJÓN JL, CAMACHO M, ROMERO DE LA OSA L, AGUILAR A & SANTAMARÍA C. 2005. Effect of carbon and nitrogen sources, pH and temperature on in vitro culture of several isolates of *Amanita caesarea* (Scop.:Fr.) Pers. *Mycorrhiza* 16: 133–136. <https://doi.org/10.1007/s00572-005-0025-6>.
- DOMÍNGUEZ-NÚÑEZ JA, BERROCAL-LOBO M & ALBANESI AS. 2019. Ectomycorrhizal Fungi: Role as Biofertilizers in Forestry. *Soil Biology* 55: 67–82. https://doi.org/10.1007/978-3-030-18933-4_4.
- DRAKE JE, GALLET-BUDYNEK A, HOFMOCKEL KS ET AL. 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO₂. *Ecology Letters* 14: 349–357. <https://doi.org/10.1111/j.1461-0248.2011.01593.x>.
- ELLSWORTH DS, ANDERSON IC, CROUS KY ET AL. 2017. Elevated CO₂ does not increase eucalypt forest productivity on a low-phosphorus soil. *Nature Climate Change* 7: 279–282. <https://doi.org/10.1038/nclimate3235>.
- FINZI AC, ABRAMOFF RZ, SPILLER KS ET AL. 2015. Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. *Global Change Biology* 21: 2082–2094. <https://doi.org/10.1111/gcb.12816>.
- FRANSSON PMA, TAYLOR AFS & FINLAY RD. 2005. Mycelial production, spread and root colonisation by the ectomycorrhizal fungi *Hebeloma crustuliniforme* and *Paxillus involutus* under elevated atmospheric CO₂. *Mycorrhiza* 15: 25–31. <https://doi.org/10.1007/s00572-003-0289-7>.
- GARDNER A, ELLSWORTH DS, CROUS KY, PRITCHARD J & MACKENZIE AR. 2021. Is photosynthetic enhancement sustained through three years of elevated CO₂ exposure in 175-year-old *Quercus robur*? *Tree Physiology* 42: 130–144. <https://doi.org/10.1093/treephys/tpab090>.
- GEHRING C, FLORES-RENTERÍA D, STHULTZ CM ET AL. 2014. Plant genetics and interspecific competitive interactions determine ectomycorrhizal fungal community responses to climate change. *Molecular Ecology* 23: 1379–1391. <https://doi.org/10.1111/mec.12503>.
- HAGENBO A, PIÑUELA Y, CASTAÑO C ET AL. 2020. Production and turnover of mycorrhizal soil mycelium relate to variation in drought conditions in Mediterranean *Pinus pinaster*, *Pinus sylvestris* and *Quercus ilex* forests. *New Phytologist* 230: 1609–1622. <https://doi.org/10.1111/nph.17012>.
- HAGENBO A, KYASCHENKO J, CLEMMENSEN KE, LINDAHL BD & FRANSSON P. 2018. Fungal community shifts underpin declining mycelial production and turnover across a *Pinus sylvestris* chronosequence. *Journal of Ecology* 106: 490–501. <https://doi.org/10.1111/1365-2745.12917>.
- HÖGBERG MN & HÖGBERG P. 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytologist* 154: 791–795. <https://doi.org/10.1046/j.1469-8137.2002.00417.x>.
- HÖGBERG MN, HÖGBERG P, MYROLD DD. 2007. Is microbial community composition in boreal forest soils determined by pH, C-to-N ratio, the trees, or all three? *Oecologia* 150: 590–601.
- HU S, TU C, CHEN X & GRUVER JB. 2006. Progressive N limitation of plant response to elevated CO₂: a microbiological perspective. *Plant Soil* 289: 47–58. <https://doi.org/10.1007/s11104-006-9093-4>.
- HUANG X-F, CHAPARRO JM, REARDON KF, ZHANG R, SHEN Q & VIVANCO JM. 2014. Rhizosphere interactions: root exudates, microbes, and microbial communities. *Botany* 92: 267–275. <https://doi.org/10.1139/cjb-2013-0225>.
- HUNGATE BA, CHAPIN III FS, ZHONG H, HOLLAND EA & FIELD CB. 1997. Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. *Oecologia* 109: 149–153. <https://doi.org/10.1007/s004420050070>.
- JIANG D, CHEN L, XIA N, NORGBEY E, KOOMSON DA & DARKWAH WK. 2020a. Elevated atmospheric CO₂ impact on carbon and nitrogen transformations and microbial community in replicated wetland. *Ecological Processes* 9: 57. <http://dx.doi.org/10.1186/s13717-020-00267-0>.
- JIANG M, MEDLYN BE, DRAKE JE ET AL. 2020b. The fate of carbon in a mature forest under carbon dioxide enrichment. *Nature* 580: 227–231. <https://doi.org/10.1038/s41586-020-2128-9>.
- JÖRGENSEN K, CLEMMENSEN KE, WALLANDER H & LINDAHL BD. 2022. Do ectomycorrhizal exploration types reflect mycelial foraging strategies? *New Phytologist*

- 237: 576–584. <https://doi.org/10.1111/nph.18566>.
- KHOO HP. 1977. The geology of Sungai Tekai area, Pahang. Pp 93–103 in *Annual Report for 1976*. Geological Survey of Malaysia Ministry of Primary Industries, Malaysia.
- LEAKE JR, JOHNSON D, DONNELLY D, MUCKLE GE, BODDY L & READ DJ. 2004. Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agro-ecosystem functioning. *Canadian Journal of Botany* 82: 1016–1045. <https://doi.org/10.1139/cjb-2013-0290>.
- LEHTO T & ZWIAZEK JJ. 2011. Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza*. 21: 71–90. <https://doi.org/10.1007/s00572-010-0348-9>.
- LEMORDANT L, GENTINE P, SWANN AS, COOK BI & SCHEFF J. 2018. Critical impact of vegetation physiology on the continental hydrologic cycle in response to increasing CO₂. *Proceedings of the National Academy of Sciences of the United States of America* 115: 4093–4098. <https://doi.org/10.1073/pnas.1720712115>.
- LI J, SUN B, LIU C ET AL. 2023. Legacy effect of long-term elevated CO₂ and warming on soil properties controls soil organic matter decomposition. *Agriculture* 13: 639. <https://doi.org/10.3390/agriculture13030639>.
- LIN G, MCCORMACK ML, MA C & GUO D. 2017. Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *New Phytologist* 213: 1440–1451. <https://doi.org/10.1111/nph.14206>.
- LINDAHL BD, IHRMARK K, BOBERG J ET AL. 2006. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. *New Phytologist* 173: 611–620. <https://doi.org/10.1111/j.1469-8137.2006.01936.x>.
- LIU J, APPIAH-SEFAH G & APREKU TO. 2018. Effects of elevated atmospheric CO₂ and nitrogen fertilization on nitrogen cycling in experimental riparian wetlands. *Water Science and Engineering* 11: 39–45. <https://doi.org/10.1016/j.wse.2017.05.005>.
- LÓPEZ-GARCÍA Á, VARELA-CERVERO S, VASAR M, DPIK M, BAREA JM & AZCÓN-AGUILAR C. 2017. Plant traits determine the phylogenetic structure of arbuscular mycorrhizal fungal communities. *Molecular Ecology* 26: 6948–6959. <https://doi.org/10.1111/mec.14403>.
- LUO H, XU H, CHU C, HE F & FANG S. 2020. High temperature can change root system architecture and intensify root interactions of plant seedlings. *Frontiers in Plant Science* 11: 160. <https://doi.org/10.3389/fpls.2020.00160>.
- LUO Y, HUI D & ZHANG D. 2006. Elevated CO₂ stimulates net accumulations of carbon and nitrogen in land ecosystems: A meta-analysis. *Ecology* 87: 53–63. <https://doi.org/10.1890/04-1724>.
- MADHU M & HATFIELD JL. 2013. Dynamics of plant root growth under increased atmospheric carbon dioxide. *Agronomy Journal* 105: 657–669. <https://doi.org/10.2134/agronj2013.0018>.
- MANOKARAN N, ABD RAHMAN K, AZMAN H, QUAH ES & CHONG PF. 1992. Short-term population dynamics of dipterocarp trees in a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forests Science* 5: 97–112.
- MARRYANNA L, AZIAN M, SUWA R, NORSHEILLA JC & SITI-AISHAH S. 2019. The study on transpiration and water use efficiency of *Shorea parvifolia* under elevated carbon dioxide concentration in the tropical forest. *International Journal of Agriculture Forestry and Plantation* 8: 98–105.
- MARRYANNA L, NOGUCHI S, KOSUGI Y ET AL. 2019. Spatial distribution of soil moisture and its influence on stand structure in a lowland dipterocarp forest in Peninsular Malaysia. *Journal of Tropical Forest Science* 31: 135–150. <https://doi.org/10.26525/jtfs2019.31.2.135150>.
- MASANO H, ALRASJID Z & HAMZAH. 1987. Planting trials of dipterocarps species outside their natural distributional range in the Haurbentes experimental forest, West Java. Pp 19–37 in Kosterman AJGH (ed) *Proceedings of the third-round table conference on dipterocarps*.
- NAING AH, JEON SM, PARK JS, KIM CK. 2016. Combined effects of supplementary light and CO₂ on rose growth and the production of good quality cut flowers. *Canadian Journal of Plant Science* 96: 503–510. <https://doi.org/10.1139/cjps-2015-0304>.
- NEHLS U & PLASSARD C. 2018. Nitrogen and phosphate metabolism in ectomycorrhizas. *New Phytologist* 220: 1047–1058. <https://doi.org/10.1111/nph.15257>.
- NING C, MUELLER G, EGERTON-WARBURTON L, WILSON A, YAN W & XIANG W. 2018. Diversity and enzyme activity of ectomycorrhizal fungal communities following nitrogen fertilization in an urban-adjacent pine plantation. *Forests* 9: 99. <https://doi.org/10.3390/f9030099>.
- NORBY RJ & ZAK DR. 2011. Ecological lessons from Free-Air CO₂ Enrichment (FACE) experiments. *Annual Review of Ecology, Evolution, and Systematics* 42: 181–203. <https://doi.org/10.1146/annurev-ecolsys-102209-144647>.
- NORSHEILLA MJC, AZIAN M, ISMAIL P, WAN MOHD SHUKRI WA & SAMSUDIN M. 2018. *Manual system Free Air CO₂ Enrichment*. Institut Penyelidikan Perhutanan Malaysia: Gigabit Communication, Puchong.
- NURUL HIDAYAH CM, LATIFF A, AHMAD FITRI Z, NIZAM MS & NUR 'AQILAH MB. 2020. Tree community structure and diversity of *Shorea lumutensis* (Balau Putih) dominated forest at Segari Melintang Forest Reserve, Perak. *Pertanika Journal of Tropical Agricultural Science* 43: 315 – 326.
- OREN R, ELLSWORTH DS, JOHNSEN KH ET AL. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* 411: 469–472. <https://doi.org/10.1038/35078064>.
- OSTROWSKA A & POREBSKA G. 2015. Assessment of the C/N ratio as an indicator of the decomposability of organic matter in forest soils. *Ecological Indicators* 49: 104–109. <https://doi.org/10.1016/j.ecolind.2014.09.044>.
- PAN T, WANG Y, WANG L, DING J, CAO Y & QIN G. 2020. Increased CO₂ and light intensity regulate growth

- and leaf gas exchange in tomato. *Physiologia plantarum* 168: 694–708. <http://dx.doi.org/10.1111/ppl.13015>.
- PAOLI GD, CURRAN LM & ZAK DR. 2005. Phosphorus efficiency of aboveground productivity in Bornean rain forest: evidence against the unimodal response efficiency hypothesis. *Ecology* 86: 1548–1561. <https://doi.org/10.1890/04-1126>.
- PARRENT JL & VILGALYS R. 2007. Biomass and compositional responses of ectomycorrhizal fungal hyphae to elevated CO₂ and nitrogen fertilization. *New Phytologist* 176: 164–174. <https://doi.org/10.1111/j.1469-8137.2007.02155.x>.
- PEAY KG, KENNEDY PG, DAVIES SJ, TAN S & BRUNS TD. 2010. Potential link between plant and fungal distributions in a dipterocarp rainforest: Community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone. *New Phytologist* 185: 529–542. <https://doi.org/10.1111/j.1469-8137.2009.03075.x>.
- PIÑERO MC, PÉREZ-JIMÉNEZ M, LÓPEZ-MARÍN J & DEL AMOR FM. 2017. Fruit quality of sweet pepper as affected by foliar Ca applications to mitigate the supply of saline water under a climate change scenario. *Journal of Science Food Agriculture* 98: 1071–1078. <https://doi.org/10.1002/jsfa.8557>.
- PRITCHARD SG, STRAND AE, MCCORMACK ML, DAVIS MA & OREN R. 2008. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO₂-enrichment. *Global Change Biology* 14: 1252–1264. <https://doi.org/10.1111/j.1365-2486.2008.01569.x>.
- SCHLESINGER WH, BERNHARDT ES, DELUCIA EH ET AL. 2006. The Duke Forest FACE experiment: CO₂ enrichment of a loblolly pine forest. In Ndsberger J, Long SP, Norby RJ, Stitt M, Hendrey GR & Blum H (eds) *Managed Ecosystems and CO₂. Ecological Studies* volume 187. Springer, Berlin, Heidelberg. https://doi.org/10.1007/3-540-31237-4_11.
- SHI J, WANG X & WANG E. 2023. Mycorrhizal symbiosis in plant growth and stress adaptation: from genes to ecosystems. *Annual Review of Plant Biology* 74: 569–607. <https://doi.org/10.1146/annurev-arplant-061722-090342>.
- SMITH SE & READ DJ. 2010. *Mycorrhizal symbiosis*. Academic Press: Cambridge.
- SOUDZILOVSKAIA NA, HEIJDENVAN DER MGA, CORNELISSEN JHC ET AL. 2015. Quantitative assessment of the differential impacts of arbuscular and ectomycorrhiza on soil carbon cycling. *New Phytologist* 208: 280–293. <https://doi.org/10.1111/nph.13447>.
- STEIDINGER BS, CROWTHER TW, LIANG J ET AL. 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* 569: 404–408. <https://doi.org/10.1038/s41586-019-1128-0>.
- STERKENBURG E, BAHR A, BRANDSTRÖM DURLING M, CLEMMENSEN KE & LINDAHL BD. 2015. Changes in fungal communities along a boreal forest soil fertility gradient. *New Phytologist* 207: 1145–1158. <https://doi.org/10.1111/nph.13426>.
- SUKRI RS, WAHAB RA, SALIM KA & BURSLEM DF. 2012. Habitat associations and community structure of dipterocarps in response to environment and soil conditions in Brunei Darussalam, northwest Borneo. *Biotropica* 44: 595–605. <https://doi.org/10.1111/j.1744-7429.2011.00837.x>.
- SWATY RL, DECKERT RJ, WHITHAM, TG & GEHRING CA. 2004. Ectomycorrhizal abundance and community composition shifts with drought: predictions from tree rings. *Ecology* 85: 1072–1084. <http://dx.doi.org/10.1890/03-0224>.
- TARIN MWK, FAN L, XIE D ET AL. 2021. Response of soil fungal diversity and community composition to varying levels of bamboo biochar in red soils. *Microorganisms* 9: 1385. <https://doi.org/10.3390/microorganisms9071385>.
- TER BRAAK CJF. 1986 Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- TER BRAAK CJF. 1990. *Update notes: Canoco version 3.10*. Agricultural Mathematics Group, Wageningen, The Netherlands.
- TERRER C, PHILLIPS RP, HUNGATE BA ET AL. 2021. A trade-off between plant and soil carbon storage under elevated CO₂. *Nature* 591: 599–603. <https://doi.org/10.1038/s41586-021-03306-8>.
- TERRER C, VICCA S, HUNGATE BA, PHILLIPS RP & PRENTICE IC. 2016. Mycorrhizal association as a primary control of the CO₂ fertilization effect. *Science* 353: 72–74. <https://doi.org/10.1126/science.aaf4610>.
- THOMPSON JB, SLOT M, DALLING JW, WINTER K, TURNER BL & ZALAMEA P. 2019. Species-specific effects of phosphorus addition on tropical tree seedling response to elevated CO₂. *Functional Ecology* 33: 1871–1881. <https://doi.org/10.1111/1365-2435.13421>.
- TRESEDER KK. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytologist* 164: 347–355. <https://doi.org/10.1111/j.1469-8137.2004.01159.x>.
- TWIEG BD, DURALL DM, SIMARD SW & JONES MD. 2009. Influence of soil nutrients on ectomycorrhizal communities in a chronosequence of mixed temperate forests. *Mycorrhiza* 19: 305–316. <https://doi.org/10.1007/s00572-009-0232-7>.
- VAN DER PUTTEN WH, BARDGETT RD, BEVER JD ET AL. 2013. Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology* 101: 265–276. <https://doi.org/10.1111/1365-2745.12054>.
- VAN TICHELEN KK & COLPAERT JV. 2000. Kinetics of phosphate absorption by mycorrhizal and non-mycorrhizal Scot pine seedlings. *Physiologia Plantarum* 110: 96–103. <https://doi.org/10.1034/j.1399-3054.2000.110113.x>.
- VEACH AM, STOKES CE, KNOEPP J, JUMPPONEN A & BAIRD R. 2018. Fungal communities and functional guilds shift along an elevational gradient in the southern Appalachian Mountains. *Microbial Ecology* 76: 156–168. <https://link.springer.com/article/10.1007/s00248-017-1116-6>.
- WALKER AP, DE KAUWE MG, BASTOS A ET AL. 2021. Integrating the evidence for a terrestrial

- carbon sink caused by increasing atmospheric CO₂. *New Phytologist* 229: 2413–2445. <https://doi.org/10.1111/nph.16866>.
- WANG C, SUN Y, CHEN HY & RUAN H. 2021. Effects of elevated CO₂ on the C stoichiometry of plants, soils, and microorganisms in terrestrial ecosystems. *Catena* 201: 105219. <https://doi.org/10.1016/j.catena.2021.105219>.
- WANG J, HASEGAWA T, LI L, LAM SK, ZHANG X & LIU X. 2019. Changes in grain protein and amino acids composition of wheat and rice under short-term increased [CO₂] and temperature of canopy air in a paddy from East China. *New Phytologist* 222: 726–734. <https://doi.org/10.1111/nph.15661>.
- WANG T, CAO X, CHEN M ET AL. 2022. Effects of soil acidification on bacterial and fungal communities in the Jiaodong Peninsula, Northern China. *Agronomy* 12: 927. <https://doi.org/10.3390/agronomy12040927>.
- WANG X, QU L, MAO Q ET AL. 2015. Ectomycorrhizal colonization and growth of the hybrid larch F 1 under elevated CO₂ and O₃. *Environmental Pollution* 197: 116–126. <https://doi.org/10.1016/j.envpol.2014.11.031>.
- WEATHER AND CLIMATE 2022. <https://weather-and-climate.com/>.
- WIDIYATNO, SOEKOTJO, NAIEM M, PURNOMO S & SETIYANTO PE. 2014. Early performance of 23 dipterocarp species planted in logged-over rainforest. *Journal of Tropical Forest Science* 26: 259–266.
- WONG-BAJRACHARYA J, CASTAÑEDA-GÓMEZ L, PLETT KL, ANDERSON IC, CARRILLO Y & PLETT JM. 2020. Untangling the effect of roots and mutualistic ectomycorrhizal fungi on soil metabolite profiles under ambient and elevated carbon dioxide. *Soil Biology and Biochemistry*: 108021. <https://doi.org/10.1016/j.soilbio.2020.108021>.
- ZAK DR, PELLITTER PT, ARGIROFF WA ET AL. 2019. Exploring the role of ectomycorrhizal fungi in soil carbon dynamics. *New Phytologist* 223: 33–39. <https://doi.org/10.1111/nph.15679>.
- ZHANG K, SU YZ & YANG R. 2019. Variation of soil organic carbon, nitrogen, and phosphorus stoichiometry and biogeographic factors across the desert ecosystem of Hexi Corridor, northwestern China. *Journal Soils Sediments* 19: 49–57. <https://doi.org/10.1007/s11368-018-2007-2>.
- ZHANG T, WANG NF, LIU HY, ZHANG YQ & YU LY. 2016. Soil pH is a key determinant of soil fungal community composition in the Ny-Ålesund Region, Svalbard (High Arctic). *Frontiers Microbiology* 7: 227. <https://doi.org/10.3389/fmicb.2016.00227>.
- ZHENG SM, XIA YH, HU YJ ET AL. 2021a. Stoichiometry of carbon, nitrogen, and phosphorus in soil: effects of agricultural land use and climate at a continental scale. *Soil and Tillage Research* 209: 104903. <https://doi.org/10.1016/j.still.2020.104903>.
- ZIEGLER C, KULAWSKA A, KOURMOULI A ET AL. 2023. Quantification and uncertainty of root growth stimulation by elevated CO₂ in a mature temperate deciduous forest. *Science of Total Environment* 854: 158661. <https://doi.org/10.1016/j.scitotenv.2022.158661>.