Tradeoffs Between Aboveground and Soil Carbon Accumulation Following Forestation

By

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Abstract

Recent decades have seen a rapid increase in global warming due to anthropogenic greenhouse gas emissions. One prevalent climate change mitigation strategy is tree planting, as trees sequester large amounts of carbon in their aboveground biomass. However, there is emerging evidence that under some conditions, soil carbon decreases following forestation, offsetting the carbon accumulated aboveground and rendering carbon sequestration efforts ineffective. The factors driving these changes in net ecosystem carbon are currently unknown. Here, we conducted a global meta-analysis on the factors affecting aboveground biomass versus soil carbon (SOC) accumulation following forestation in grasslands and croplands. We considered the effects of prior land use, regrowth strategy, mycorrhizal associations, and environmental factors on total ecosystem carbon and SOC accumulation over time. Results indicate that while there is a tradeoff between SOC and aboveground carbon accumulation, the loss of SOC does not negate the increase in aboveground carbon following forestation. Sites with low initial SOC before forest establishment accumulate more SOC than sites with high SOC, regardless of prior land use. Overall, forest stand age, prior land use, regrowth strategy, and mycorrhizal associations drive carbon accumulation over time and should be considered in the context of future forestation projects implemented for carbon sequestration.

Thesis supervisor: César Terrer
Title: Assistant Professor of Civil and Environmental Engineering

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Introduction

1.1 Background and Motivation

Climate change has entered the international stage as one of the greatest threats to humanity in the 21st century. In 2015, the Paris Agreement was established with the goal of keeping global mean temperatures below 1.5°C higher than pre-industrial levels through a variety of mitigation strategies (Paris Agreement, 2015). Natural climate solutions are crucial to reaching this goal, potentially accounting for up to 37% of atmospheric carbon dioxide removal through 2030 (Griscom et al., 2017). Forestation is one prevalent mitigation method, as forests are cost-efficient carbon (C) sinks and forestation may capture an additional 205 Gt of C globally (Bastin et al., 2019).

Worldwide, forests contain 650 Gt of C distributed across their soils, aboveground biomass (AGB), and litter (FAO, 2010). However, while forestation increases the quantity of C stored in the AGB, its effects on soil C accumulation are less known. Surprisingly, one repeated sampling study located in a Scottish moorland reported that soil C quantities decreased following forestation, which negated the increases in C stored in the AGB and resulted in no net ecosystem increase in C stock (Friggens et al., 2020). Currently, it is unclear the extent to which biological and anthropogenic factors impact C accumulation rates in AGB versus in the soil.

Prior studies have identified tree mycorrhizal associations (Friggens et al., 2020; Terrer et al., 2021), tree species (Hou et al., 2019; Guo and Gifford, 2002; Li et al., 2012), prior land use (Bukoski et al., 2022), and biome type (Cook-Patton et al., 2020) as factors affecting soil organic carbon (SOC) stock following forestation, but a comprehensive analysis of the drivers of SOC accumulation has not yet been conducted. Hence, the novelty of our study lies in the incorporation of both aboveground C and SOC stocks into our meta-analysis. We examine how

SOC accumulates as a function of AGB and analyze the factors driving SOC and net ecosystem C accrual. Our study is focused on C accumulation in grasslands as croplands, as these are the two main potential afforestation sites (Humpenöder et al., 2014).

We predict that sites with a low initial SOC stock will have higher C sequestration rates following forest establishment. In croplands, which contain C-depleted soils, we predict that SOC will increase as AGB increases. Meanwhile, we predict the SOC in C-rich grassland soils will decrease because of higher rates of soil priming and C turnover following forestation. The results of this study will improve our knowledge of the optimal management practices and sites in which maximum C sequestration can occur.

1.2 Thesis Objectives

The purpose of this thesis is to determine the factors driving AGB vs. SOC accumulation trends in prior grasslands and croplands. More specifically, we assess the impact of prior land use (cropland or grassland), tree mycorrhizal association, and regrowth strategy (natural regrowth or manual planting) on accumulation trends. The impact of environmental conditions including Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) are analyzed. Because regions of potential afforestation exist worldwide across Sub-Saharan Africa, Latin America, Asia, Europe, and the U.S. (Humpenöder et al., 2014), we aim to acquire a globally representative dataset to the extent possible of existing literature. We examine how SOC stock changes over time and how accumulation rates are driven by these various factors.

The results of this thesis may be used to develop a model to quantify the net ecosystem C accumulation in a region given its prior land use and other geographical information, eliminating the need for field data collection. Results of this thesis may help make informed decisions on using forestation as a nature-based C capture solution.

Literature Review

2.1 Carbon in Terrestrial Ecosystems

Terrestrial ecosystems store over half of the world's organic C (Ciais and Sabine, 2013). From an ecological perspective, forest preservation and forestation offer several benefits, including water and climate regulation (Janes-Bassett et al., 2021). In the context of global warming, nature-based climate change solutions such as forestation are necessary for limiting global warming to less than 1.5°C as stated in the Paris Agreement (IPCC, 2023; Paris Agreement, 2015). Currently, forestation and soil C sequestration are the only carbon dioxide removal methods that are utilized on a large scale, as they are economically favorable and less technologically complex than other C storage solutions (IPCC, 2023). Here, forestation refers to both afforestation – the planting of trees on land that has not historically supported forests – and reforestation – the planting of trees in historically forested regions.

2.2 Soil Organic Carbon: Sources and Distribution

Along with the C stored in AGB, there is an immense quantity of C stored in forest soil (Batjes, 2014). While some soil C is stored inorganically in the form of carbonates, a majority of C in the topsoil is stored as soil organic C (SOC), which is the largest C pool across most of the world's land area at 1,500 Gt (Scharlemann et al., 2014).

The accumulation of SOC is controlled by addition through litterfall and root turnover (Hou et al., 2019) and reduction through microbial organic matter decomposition and leaching (Jobbágy and Jackson, 2000). The rate of SOC accumulation may also depend on additional factors such as climate, landscape, soil properties, tree species and management, natural disturbances, nitrogen supply, and litter quality (Lal, 2005). Both the vertical distribution of SOC as well as the total abundance of SOC vary greatly across ecosystems. In general, SOC stock is positively correlated with precipitation and negatively correlated with temperature. Hence, the majority of SOC is stored in the northern latitudes, specifically in the northern permafrost regions (Scharlemann et al., 2014). SOC is also a function of vegetation, which influences both the total abundance of SOC and its depth profile (Jobbágy and Jackson, 2000). Ecosystems with vegetation containing most of their biomass belowground (i.e. grasslands) have most of their C reservoirs in the soil. Meanwhile, ecosystems with vegetation containing most of their biomass aboveground (i.e. tropical forests) contain more C aboveground than in the soil. In contrast, aboveground C (AGBC) accumulation occurs more rapidly in lower latitudes, such as in tropical forests, which have high precipitation levels and warmer temperatures (Cook-Patton et al., 2020; Scharlemann et al., 2014).

2.3 LULCC and Forestation on Grasslands and Croplands

Land use change (LUC) is defined as the change in management practices of a specific type of land (e.g. tillage, fertilization, logging, fire), while land cover change (LCC) is the conversion from one type of land to another (e.g. cropland to forest) (Houghton et al., 2012).

Depending on the process, LUC and LCC (referred to together as LULCC) may act as either a C source or sink. On a global scale, LULCC comprises the second-largest anthropogenic C source, accounting for 11% of anthropogenic C emissions from 2012 to 2021 (Friedlingstein et al., 2022). Some of these emissions result from a reduction in SOC stock, as LULCC can affect the abundance of soil C by influencing net primary productivity (Batjes, 2014). One meta-analysis found that the conversion of forests, grasslands, and wetlands to croplands decreased SOC stocks by an average of 25% (Beillouin et al., 2023). However, this thesis will focus on the potential of LULCC to act as a C sink by examining the conversion of grasslands and croplands to forests, as they comprise most of the land area with the potential for afforestation (Humpenöder et al., 2014).

Several sources agree that while SOC stocks may remain stagnant or even decrease in grasslands following forestation, SOC stock tends to increase in croplands (Li et al., 2012; Hong et al., 2020). This may be due to the differences in initial SOC stock in the two land types. Grasslands contain a significant amount of C in their soil compared to their AGB, and the introduction of fresh C into the soil from trees may stimulate the microbial mineralization of older C, thereby promoting a loss of SOC (Fontaine et al., 2007). Meanwhile, croplands contain low initial SOC stocks due to prior depletion from crop growth and may therefore have a greater ability to accrue more SOC following forestation. One meta-analysis reported that on average, croplands with low initial SOC experienced a 57% increase in SOC stocks following conversion to forests (Beillouin et al., 2023). Another paired plot study in northern China found that initial C stock was the most important factor driving SOC density following afforestation (Hong et al., 2020).

2.4 Other potential Drivers of SOC Accumulation Following Forestation

Aside from prior land use, there are other factors that may influence SOC accumulation following forestation. For instance, the establishment of mixed species forests increases forest productivity, which may increase C sequestration and prevent rapid SOC decomposition (Jandl et al., 2007; Rytter and Rytter, 2020). Additionally, tree species may play an important role in the rate of C sequestration since the rates of SOC accumulation and distribution vary between species (Jandl et al., 2007). Indeed, Li et al. (2012) found that C in both the mineral and organic soil layers increased following hardwood forestation, but there was no net change in soil C following softwood forestation. In contrast, Guo and Gifford (2002) found that the establishment of hardwood broadleaf plantations on pastures did not significantly affect SOC, while the planting of softwood conifer trees significantly reduced SOC. These variances may be due to the difference in growth rates between tree species (Rytter and Rytter, 2020).

Rather than the tree species themselves, it is possible that their mycorrhizal associations are the driving factor of net SOC sequestration (Friggens et al., 2020). Trees with ecto-mycorrhizal fungal associations (EcM) such as softwoods uptake more nitrogen, which can increase SOC depletion through microbial priming. Meanwhile, trees with arbuscular-mycorrhizal associations (AM) such as hardwoods produce a greater quantity of compostable litter, which acts as a long-term source of SOC (Terrer et al., 2021).

Other potential biological drivers of SOC accumulation include nitrogen fixation ability, wood density, leaf type, and tree stand age (Bukoski et al., 2022). Tree stand age has been shown to significantly and positively affects the rate of SOC accumulation, particularly in the topsoil layer (Hou et al., 2019). Forestation can significantly increase soil C up to 30-50 years after planting (Li et al., 2012), although C sequestration rates may decline after forests reach maturity (Humpenöder et al., 2014).

Methodology

In this thesis, we conducted a meta-analysis to determine the factors driving total ecosystem C and SOC accumulation and predict C accumulation over time. We first assembled a global dataset through a literature search and collected environmental data. Then, we conducted variable importance analysis to determine the main factors driving C accumulation. Lastly, we used generalized additive mixed modeling and linear mixed modeling to predict C accumulation over time under various forestation scenarios.

3.1 Global Dataset Assembly

In total, 179 studies (911 individual data points) were used in this meta-analysis. The studies analyzed in this thesis were a collection of paired plot, chronosequence, and repeated sampling studies. To obtain the articles, we conducted a literature search using the Web of Science with the keywords “aboveground carbon,” “soil carbon,” “plantation,” and “grassland”. In addition, we obtained data from Chronobase, an existing soil database compiled by the MIT Terrer Lab; a meta-analysis by Cook-Patton et al. (2020) on forest regrowth; and a meta-analysis on the changes in SOC with forest stand age (Hou et al., 2019).

To be included in this analysis, an article needed to meet several criteria. First, the study had to be conducted on a site that was previously a grassland (natural or grazed) or cropland. We recorded whether the plot underwent natural regrowth or if it was a plantation, and if there were any disturbances (i.e. fire, hurricane, landslides, logging, mining) and/or past management practices (i.e. irrigation, fertilization, thinning, weeding) prior to forestation. Second, the study needed to contain site coordinates, state the stand age of each forest plot at the time of measurement, and contain a control plot not subjected to forestation. If there were no control plots, then the study had to have included at least two forest plots with different stand ages. Third, the study had to include data on either SOC or soil organic matter (SOM) stocks and the depths at which they were measured (there were no requirements for the depth of the soil sample measurements). Tree genera were recorded but not required.

We used the Web Plot Digitizer (https://apps.automeris.io/wpd/) to extrapolate data from figures and graphs in the literature. C accumulation in the understory and litter forest layers was disregarded, as C storage in these layers was reported inconsistently.

3.2 Environmental Data Collection and Mycorrhizal Classification

To determine the Mean Annual Temperature (MAT) and the Mean Annual Precipitation (MAP) at each site, we used their geographical coordinates along with WorldClim historical climate data (https://worldclim.org). Then, we used the FungalRoot online database to determine the tree mycorrhizal associations – AM, EcM, or mixed – present in the forests (Soudzilovskaia et al., 2020). A site was classified as containing mixed mycorrhizal types if: 1) it contained both AM and EcM tree genera, 2) it contained a genus that was classified as both AM and EcM in the database (e.g. *Eucalyptus*), or 3) the study did not specify the tree genera present.

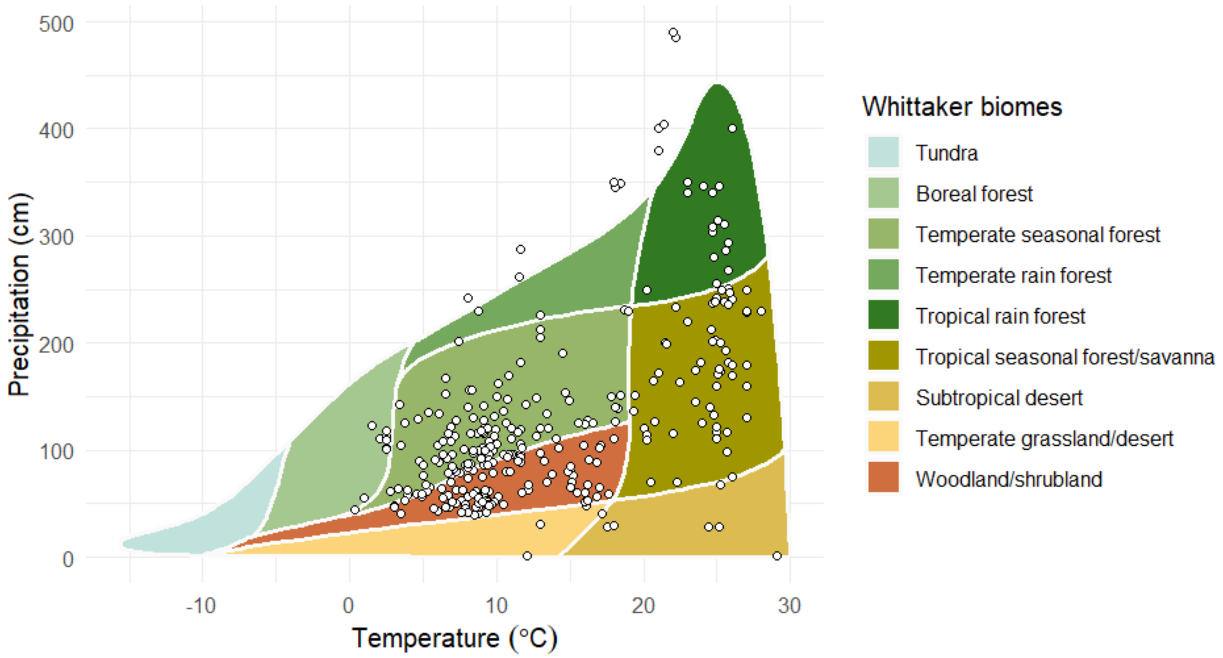


Figure 1. Distribution of sites across Whittaker biomes.

3.3 SOC Data Standardization

Because SOC was measured at varying depths across studies, we standardized SOC measurements to a uniform depth. First, all units for SOC stock were converted to Mg·ha^{-1}. For studies only containing data on SOM stocks, SOC stocks were calculated using a conversion factor of 0.58 (Pribyl, 2010). For studies that listed SOC as a fraction of soil mass, we used the soil bulk density (*BD*) to convert these values to mass of SOC per unit land area

$$SOC_a = SOC_m * BD * D \tag{1}$$

where SOC_a is the SOC stock per unit area (Mg·ha^{-1}), SOC_m is the SOC stock per unit soil mass, and *D* is the depth (cm) to which soil C is measured. When not listed in the study, *BD* was obtained using spatial data from SoilGrids (https://soilgrids.org/).

Then, we used a fitted log-curve to estimate the total SOC accumulation for each plot

$$\log\left(SOC_c\right) = K\log\left(D\right) + I \tag{2}$$

in which SOC_c is the cumulative SOC stock (Mg·ha^{-1}), K is the fitted slope parameter, and I is the fitted intercept. If the study site only listed SOC stock measurements at one depth, we used biome-specific slope parameters compiled by Jobbágy and Jackson (2000). All soil C accumulation measurements were standardized to a depth of 60 cm.

3.4 Aboveground Biomass Carbon Data Standardization and Estimation

For studies containing data on AGB, we determined the aboveground C stock present using a conversion factor of 0.47 (Aalde et al., 2006). Meanwhile, for studies lacking aboveground data, we estimated aboveground biomass C accumulation (AGBC) using the Chapman Richards growth curve

$$AGBC = 0.47 * A\left(1 - e^{\frac{-t}{b}}\right)^{c} \tag{3}$$

where A is the asymptotic accumulation, b is the growth rate, t is the forest age, and c is the shape parameter.

We considered deriving the Chapman Richards growth curve parameters for each site either from 1) tree genera or 2) geographical coordinates. To determine the potential applicability of both methods, we calculated the AGBC of sites containing field-derived AGBC using each method and compared the values. Overall, the spatially derived AGBC values were found to relate more closely to the field-derived values (see Supplementary Fig. 1) and were thus chosen for this study.

Parameters A, b, and c of the Chapman Richards curve were determined using the European Space Agency's Climate Change Initiative Biomass (CCIBM) project, which maps

AGB growth on a global scale. The CCIBM dataset has a resolution of 100 x 100 m and was generated using input from global C-band, L-band, and LIDAR remote sensing (https://climate.esa.int/en/projects/biomass/).

Following AGBC estimation, we then calculated total ecosystem C (TEC) stock

$$TEC = AGBC_t + SOC_a \tag{4}$$

where $AGBC_t$ is the C stored in the living tree biomass at time t. C stored in the understory and litter layers were excluded from the analysis.

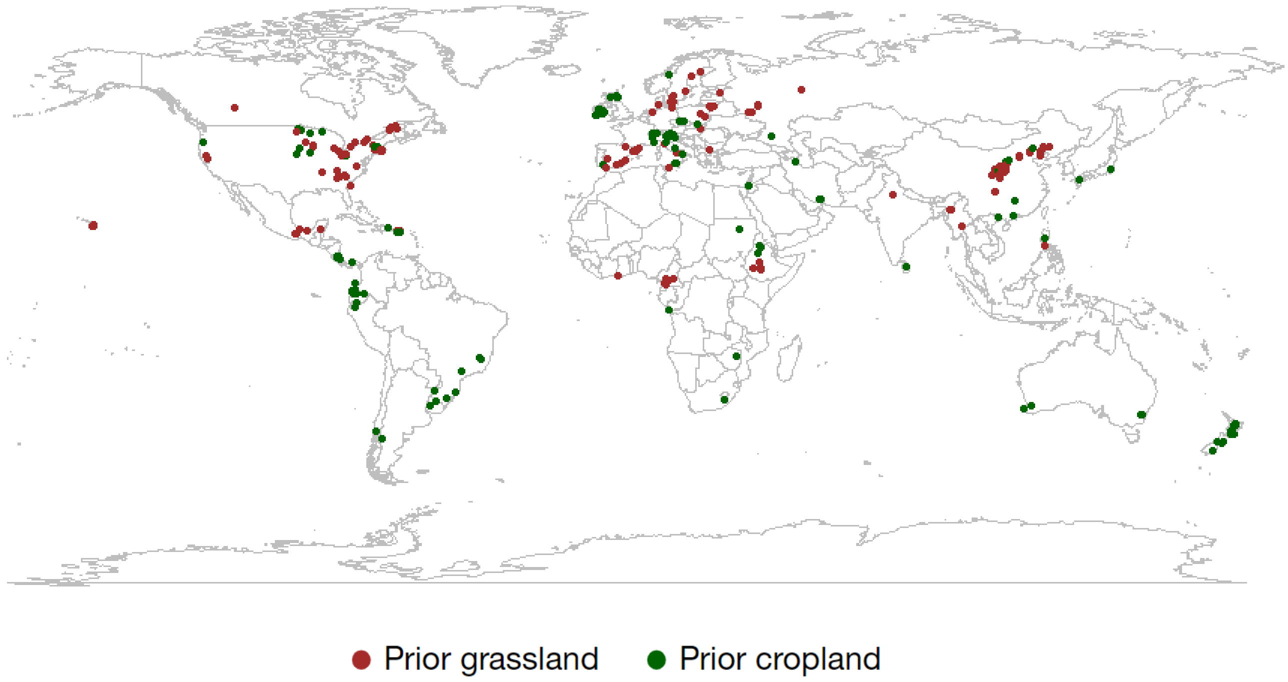


Figure 2. Spatial distribution of the study sites. Forested sites on prior grasslands are shown in green; sites on prior croplands are shown in brown.

3.5 Model Selection and Variable Importance Analysis

We modeled the effect of the interaction between forest age and AGBC accumulation on SOC accumulation using a linear mixed effect model (LMM)

$$R_i = X_i \times \beta + Z_i \times b_i + \varepsilon_i \tag{5}$$

where R_i is the richness value for each plot, X_i x β is the fixed component, Z_i x b_i is the random component, and $\varepsilon_i$is the error term. X_i and Z_i are matrices with dimensions n_i x p, where n_i is the number of observations per plot and p the number of explanatory variables (Zuur et al., 2009). Three LMMs were considered using the "lme4" R package – 1) a model with no random term, 2) a random intercept model, and 3) a random intercept and slope model – and the third model was chosen as it displayed the lowest Akaike Information Criterion (AIC).

Meanwhile, generalized additive mixed effect models (GAMMs) were generated using the "mgcv" package in R

$$Y_i = f\left(X_i\right) + Z_i \times b_i + \varepsilon_i \tag{6}$$

where Y_i is the response variable for iteration i and $f(X_i)$ is a function

$$f\left(X_i\right) = \sum_{j=1}^{p} \beta_i \times b_j\left(X_i\right) \tag{7}$$

composed of basic functions $b_j(X_i)$ (Zuur et al., 2009). Best fit GAMM selection was carried out using the dredge function from the Multi-Model Interface ("MuMIn") R package for total ecosystem C and SOC accumulation. Each dredged model included the linear main effects of forest mycorrhizal type, regrowth strategy (management type), prior land use, MAT, and MAP, as well as the interaction of each variable with forest age. (Linear interactions of MAT and MAP with forest age were used rather than smooth interactions as to avoid issues with singularity.)

The best fit models for both total ecosystem C and SOC included forest age, mycorrhizal type (*MycT*), prior land use (*LU*), and management type (*MgT*)

$$Response \quad LU + MycT + MgT + s\left(Age\right) \tag{8}$$

where *s(Age)* represents a smooth term for forest age. Models were then used to predict C accumulation under various scenarios: 1) EcM vs. AM vs. mixed mycorrhizal forests, 2) plantations vs. naturally regrowing forests, 3) forests grown on prior croplands vs grasslands, and 4) various MAT and MAP regimes. As the distributions of total ecosystem C and SOC data were both right-skewed, the data was log-transformed before model fitting to achieve a normalized distribution. We took the mean of the predictors not examined in each scenario.

Variable importance analysis was also conducted using the MuMIn dredge function; however, only the main effects of the variables rather than their interactions with forest age were considered. For both total ecosystem C and SOC accumulation, we generated GAMMs using the linear effects of prior land use, mycorrhizal type, and management type while using the smooth terms for forest age, MAT, and MAP.

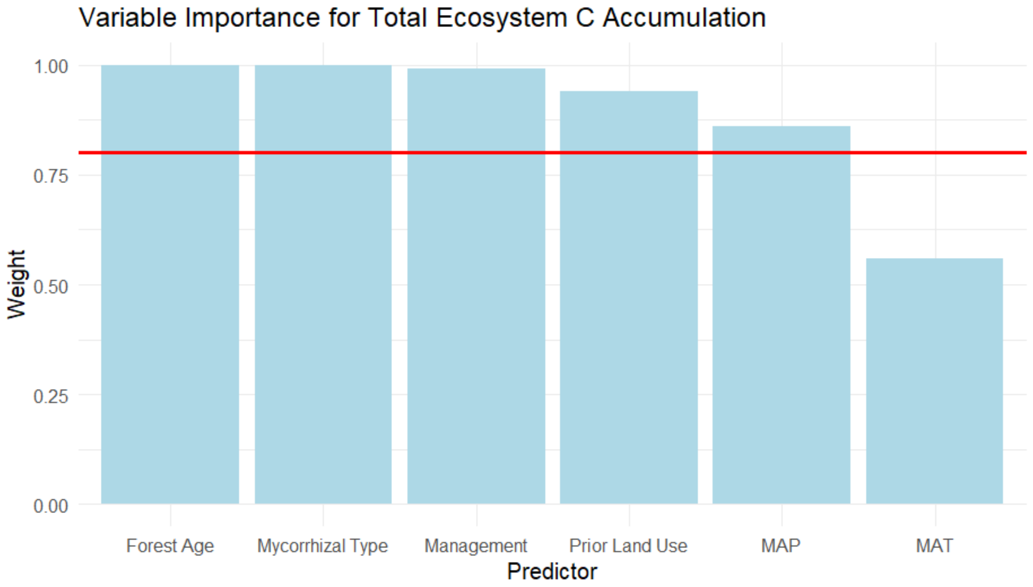
$$Response \quad LU + MycT + MgT + s\left(Age\right) + s\left(MAT\right) + s\left(MAP\right) \tag{9}$$

Variable importance was conducted using the sum of model weights, and the threshold of importance was set to 0.8.

Results

4.1 Variable Importance Analysis

Variable importance analysis revealed that forest age, mycorrhizal type, management, prior land use, and MAP were important for determining total ecosystem C accumulation. Meanwhile, forest age, mycorrhizal type, management, and prior land use affected SOC accumulation.



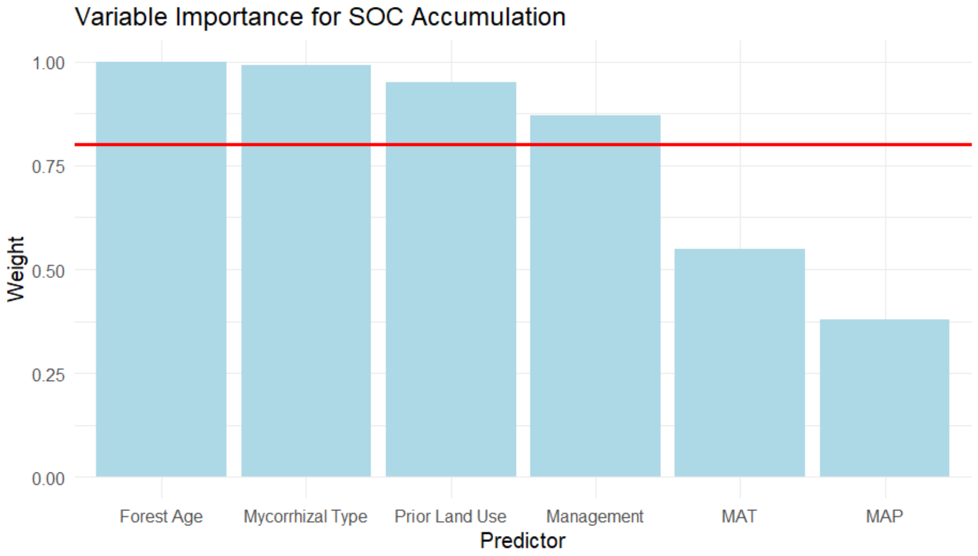


Figure 3. Variable importance analysis for total ecosystem C accumulation and SOC accumulation. The threshold of importance is established at 0.8.

Although prior land use was included in the best fit model for total ecosystem C (see Eq. 7) and revealed lower total ecosystem C accrual in prior grasslands than croplands, the effect was not statistically significant. Meanwhile, while the accumulation of total ecosystem C was the lowest in mixed mycorrhizal forests < EcM forests < AM forests, the effect of mycorrhizal type was not significant across all three categories.

Regarding SOC accumulation, neither the effects of management type nor forest mycorrhizal type were statistically significant. However, forests established on prior grasslands were shown to have accumulated significantly less SOC than croplands ($p < 0.05$). Forest age was shown to have a significant effect ($p < 0.001$) on both total ecosystem C and SOC accumulation.

Despite variations in statistical significance, total ecosystem C and SOC accumulation under different mycorrhizal associations, prior land uses, and management types were still modeled to enhance our understanding of the ways in which these factors may drive C accrual trends that may not be captured by their p-values alone.

4.2 Total Ecosystem Carbon Accumulation

Overall, we found a positive ecosystem C accumulation trend over time following forestation (See Fig. 4). Total ecosystem C accumulated most rapidly in the first few decades after forest establishment. However, C accumulation did not stabilize over time, indicating the potential for forests to accumulate C long after establishment.

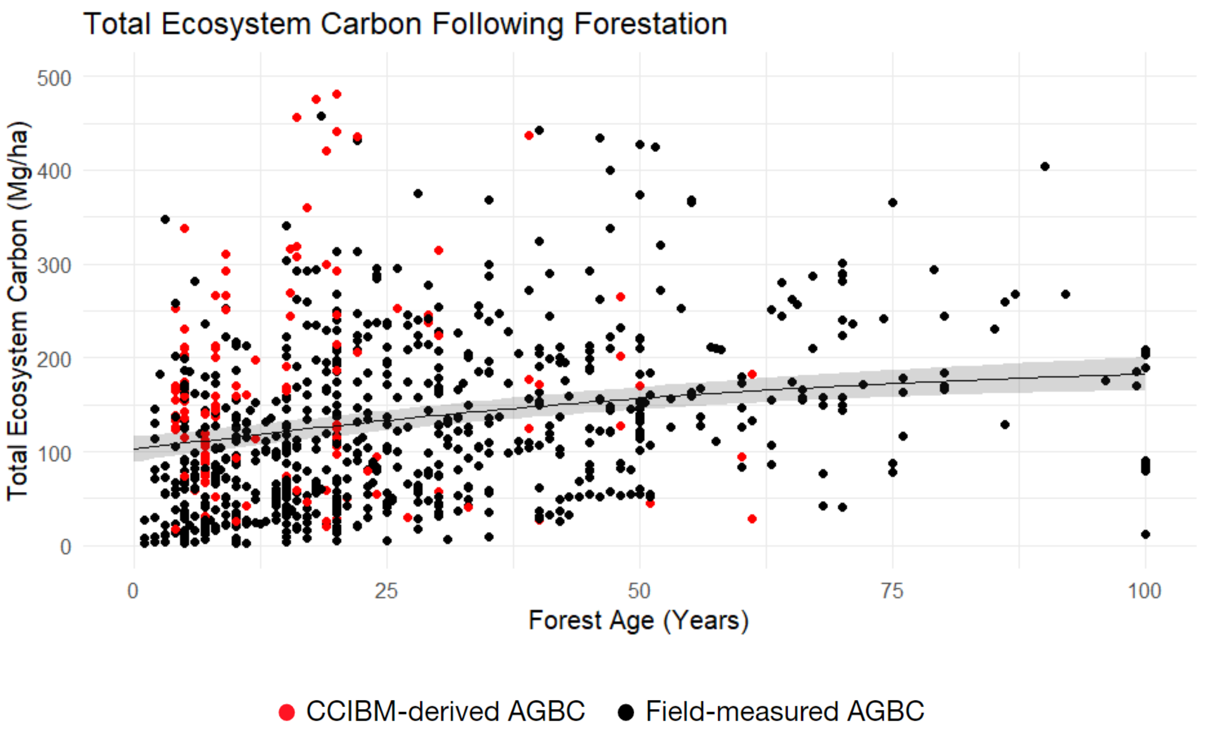


Figure 4. GAMM of total ecosystem C accumulation over time, with age as a predictor. Values with field-measured AGBC are shown in red; values with CCIBM-derived AGBC measurements are shown in black.

Figure 5 displays the percentage of total ecosystem C stored in the AGB over time. On the individual level, there was considerable variability in the proportion of C stored in the AGB, especially in younger forests. The distribution of C storage spanned from nearly all C being sequestered in the soil to almost entirely in the AGB. Nevertheless, the overall trend is consistent with the trajectory described by the Chapman Richards growth curve. While most of the C was initially stored in the soil, the proportion of C stored aboveground increased with time as the trees experienced rapid growth and began to stabilize at approximately 40% by 50 years. The result supports prior literature that suggests that SOC, rather than AGB, is the largest C sink in forests (Liu et al., 2018).

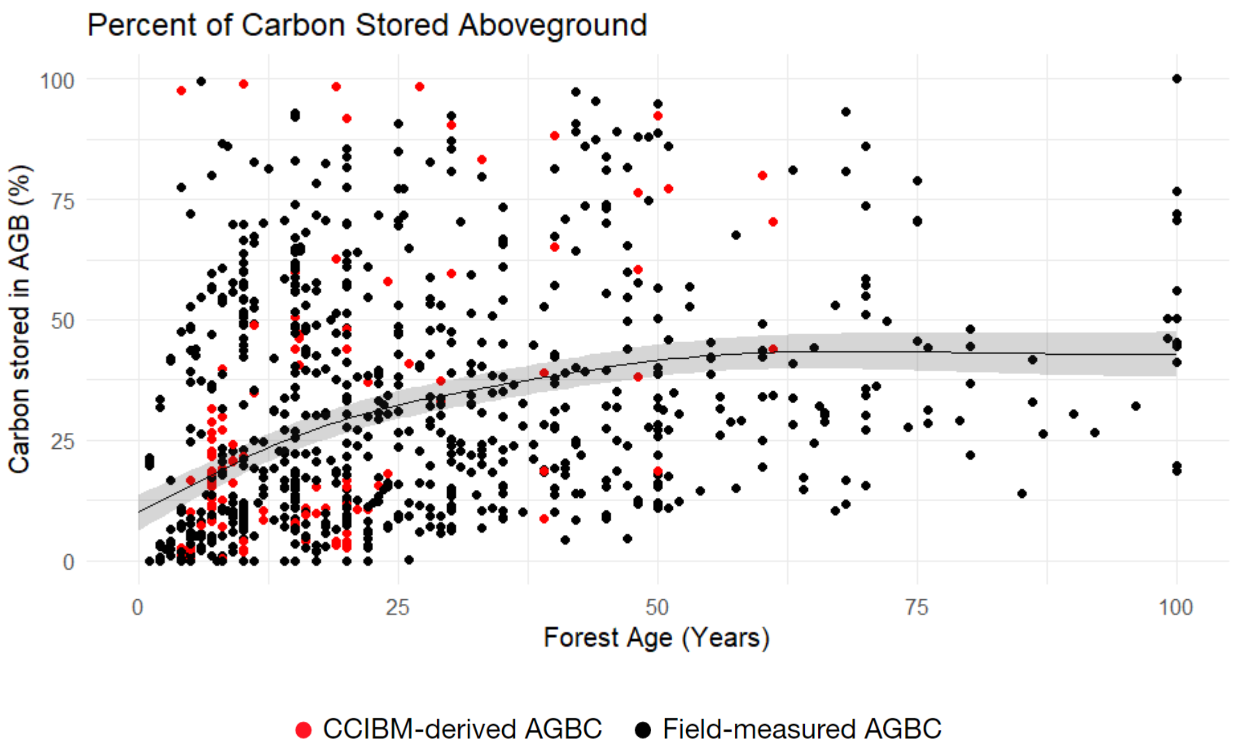


Figure 5. GAMM of the percentage of total ecosystem C stored in AGB over time, with age as a predictor. Values with field-measured AGBC are shown in red; values with CCIBM-derived AGBC measurements are shown in black.

When modeling the accumulation of AGBC compared to SOC, we found a negative correlation between AGBC and SOC accrual that interacted with forest age (see Fig. 6). In other words, as forests aged, forests that accumulated more AGBC were found to accumulate disproportionately less SOC. When AGBC stocks reached a threshold of approximately 110 $Mg{\cdot}ha^{-1}$, the forests began to experience a loss of SOC (see Fig. 7). However, the decrease in SOC accumulation did not negate the accumulation of AGBC, allowing forestation to still act as a C sink throughout time (see Fig 4).

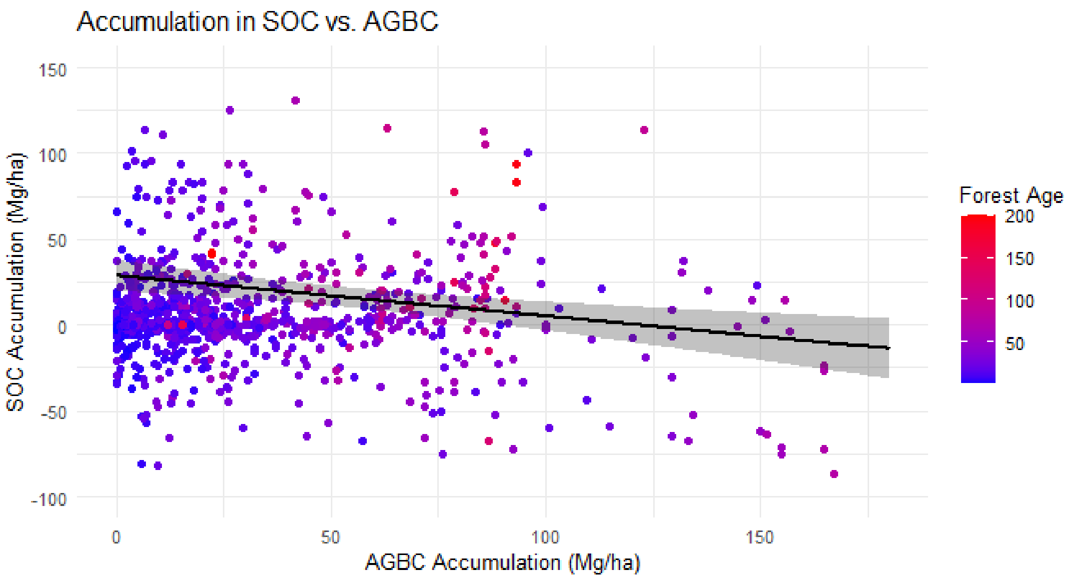


Figure 6. LMM of AGBC vs. SOC accumulation. The LMM models SOC accumulation at a forest age of 50 years.

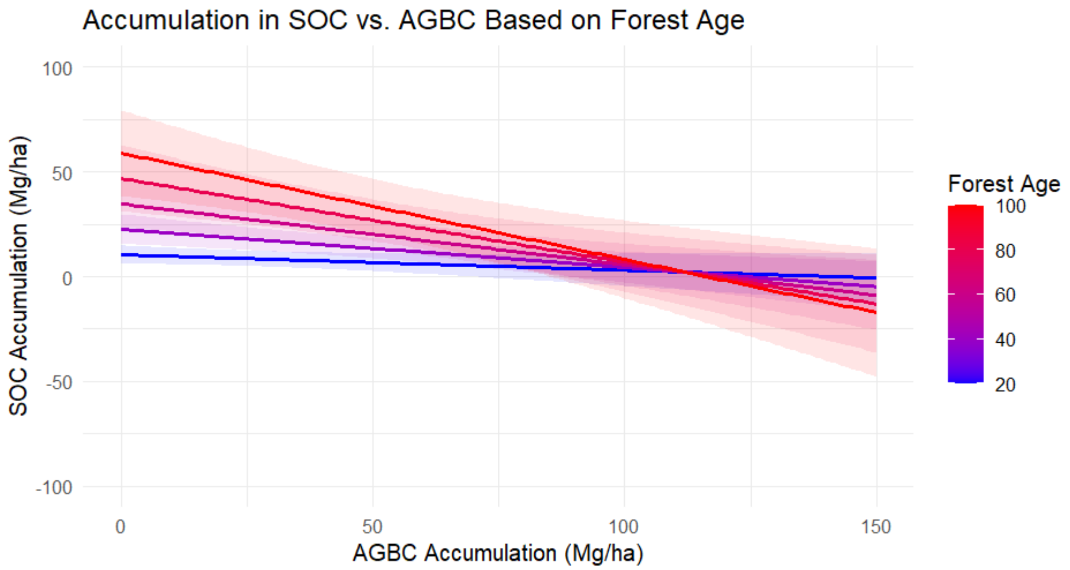


Figure 7. LMM of AGBC vs. SOC accumulation with best fitted models at varying forest ages. Models were generated using the interaction between AGBC and forest age.

4.3 Carbon Accumulation by Mycorrhizal Type

While containing less initial SOC and total ecosystem C than both EcM and mixed mycorrhizal forests, AM forests accumulated more SOC and total ecosystem C than either mycorrhizal type over the span of 60 years (see Fig. 8, Fig. 9). In contrast, neither EcM nor mixed forests demonstrated major increases in SOC. However, the forest plots containing the highest SOC abundance were EcM forests (see Fig. 9).

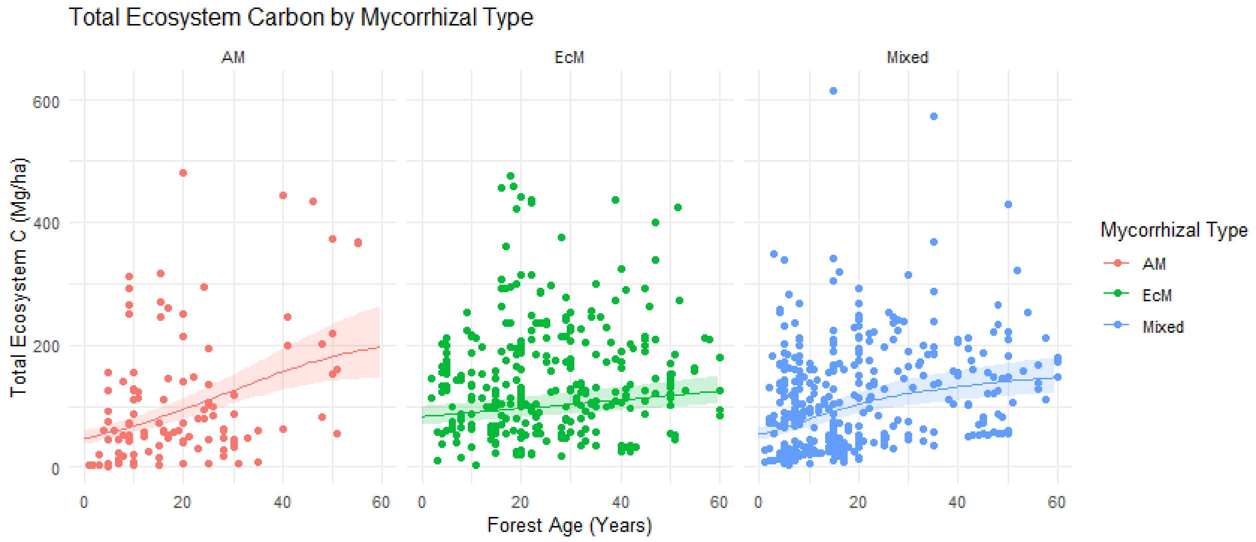


Figure 8. Total ecosystem C over time for forests of AM, EcM, and mixed mycorrhizal associations.

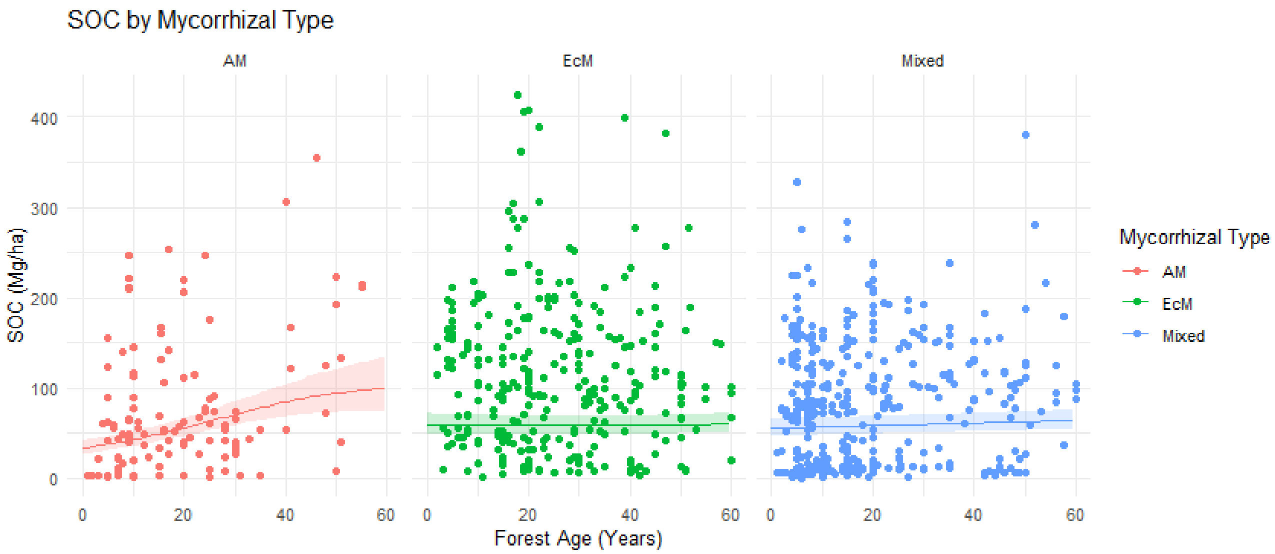


Figure 9. SOC over time for forests of AM, EcM, and mixed mycorrhizal associations.

4.4 Carbon Accumulation by Regrowth Strategy

Both naturally regrowing and planted forests demonstrated an increase of total ecosystem C over time, as well as an increase in SOC over time (see Fig. 10, Fig. 11). There were no major differences between regrowth strategies concerning the accumulation or absolute quantity of total ecosystem C.

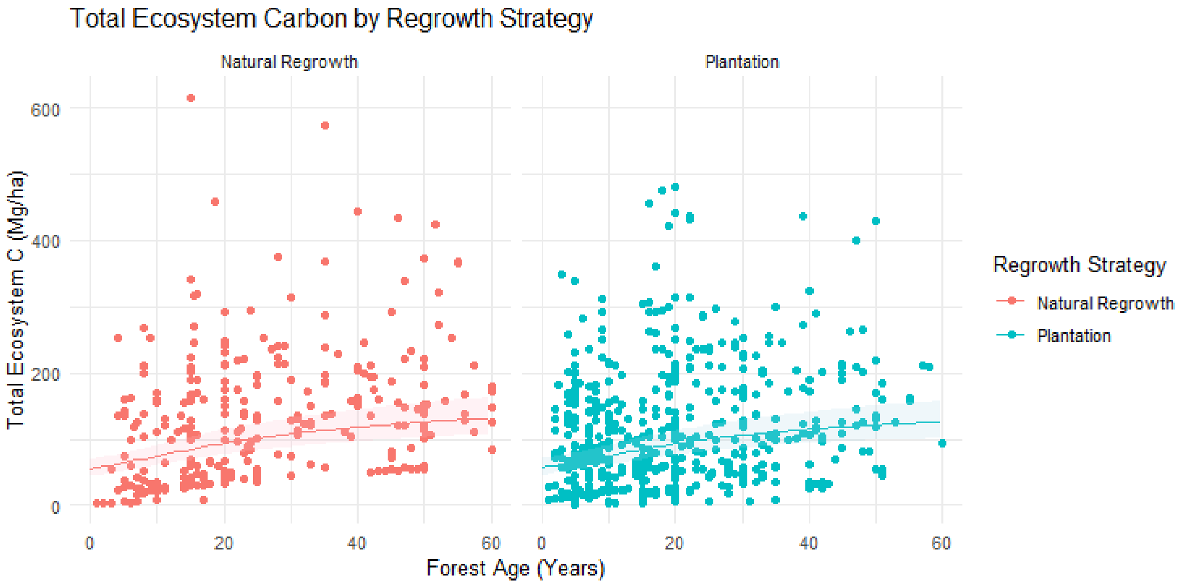


Figure 10. Total ecosystem C over time for sites that underwent natural regrowth and manual planting.

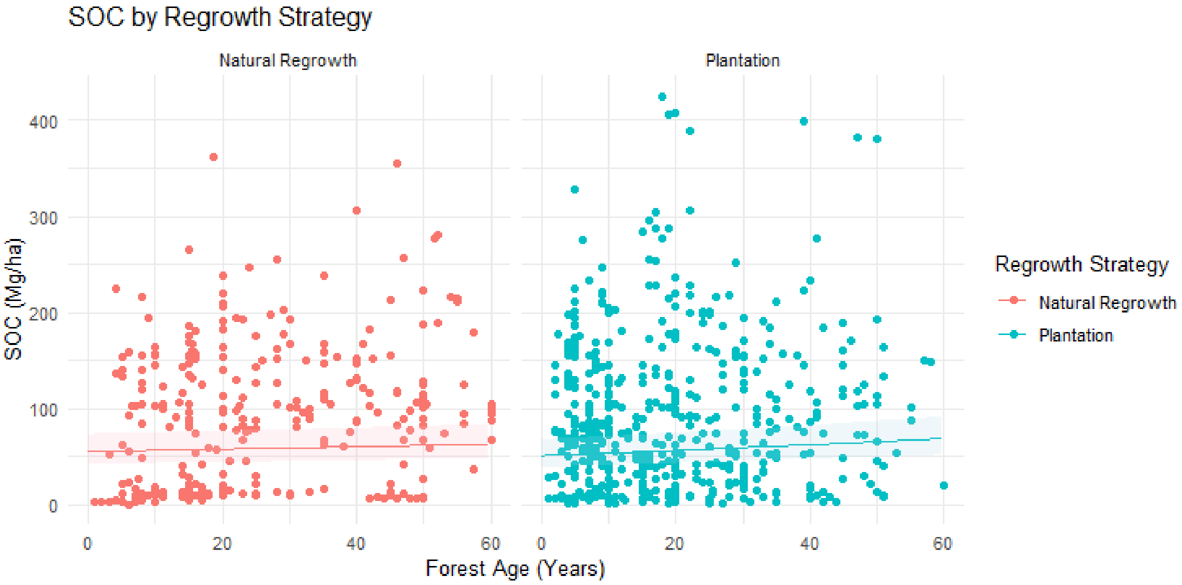


Figure 11. SOC accumulation over time for sites that underwent natural regrowth and manual planting.

4.5 Carbon Accumulation by Prior Land Use

The initial SOC stocks for both croplands and grasslands are shown in Figure 12. As predicted, grasslands were shown to have significantly higher initial SOC stocks than croplands ($p < 0.001$, Wilcoxon test).

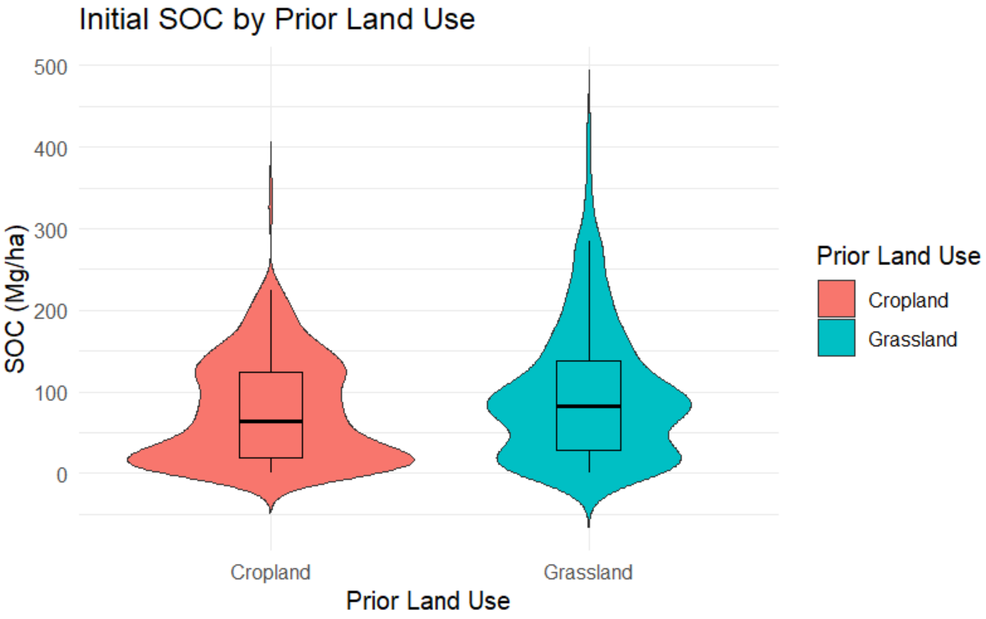


Figure 12. Initial SOC on sites that were previously croplands and grasslands. Grasslands have statistically significant higher initial SOC stocks (p < 0.001, Wilcoxon test).

The relationship between initial SOC stocks and SOC stocks following forestation for both prior croplands and grasslands is shown in Figure 13. As hypothesized, plots with initially low SOC stocks tended to accumulate more SOC following forestation, although this phenomenon occurred for both prior cropland and grassland sites irrespective of prior land use. Despite prior croplands accumulating more SOC over time compared to grasslands (see Figure 14), forests under both prior land uses demonstrated similar total ecosystem C accumulation and abundance (see Figure 15).

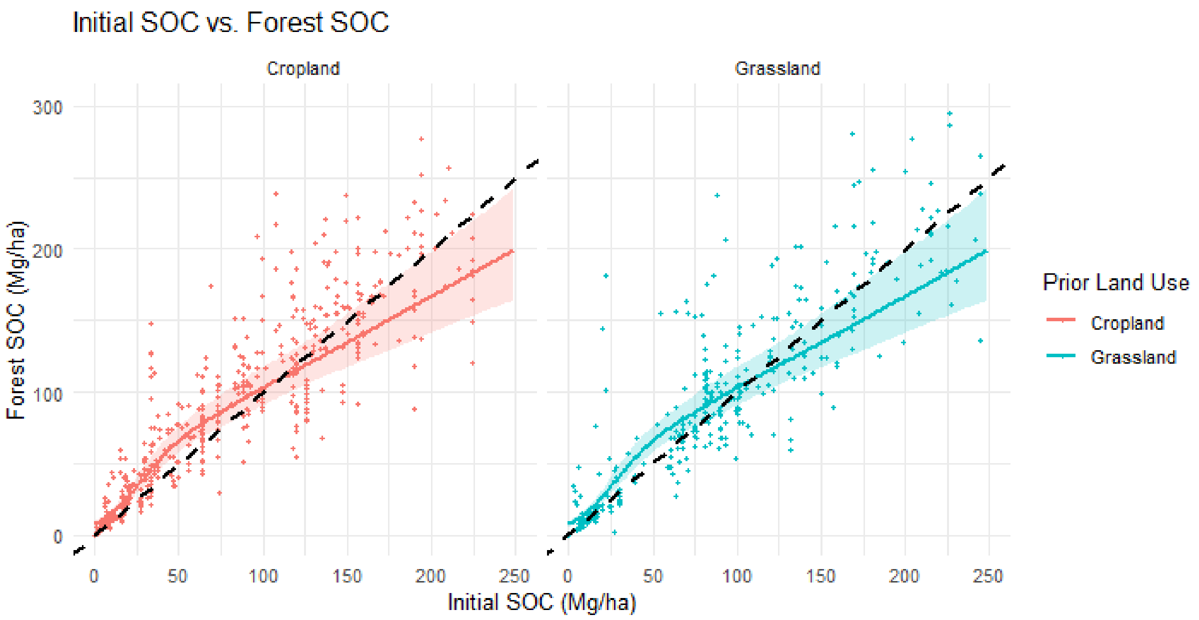


Figure 13. Initial SOC (before forestation) vs. SOC following forestation on sites established on prior croplands and grasslands. Dashed lines represent the 1:1 ratio of initial to forest SOC stock.

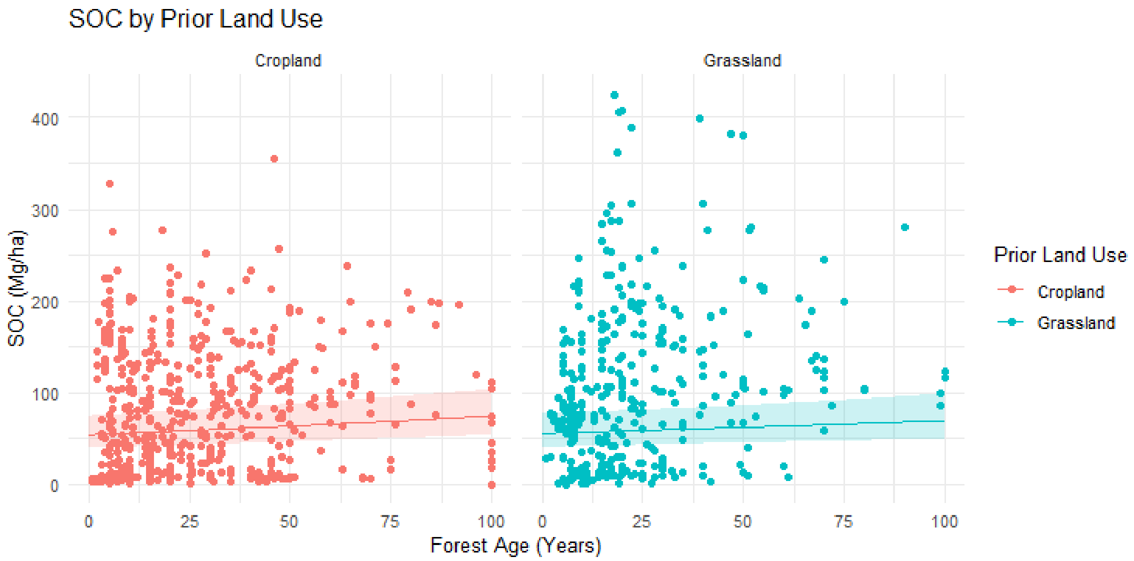


Figure 14. SOC over time on sites that were established on prior croplands and grasslands.

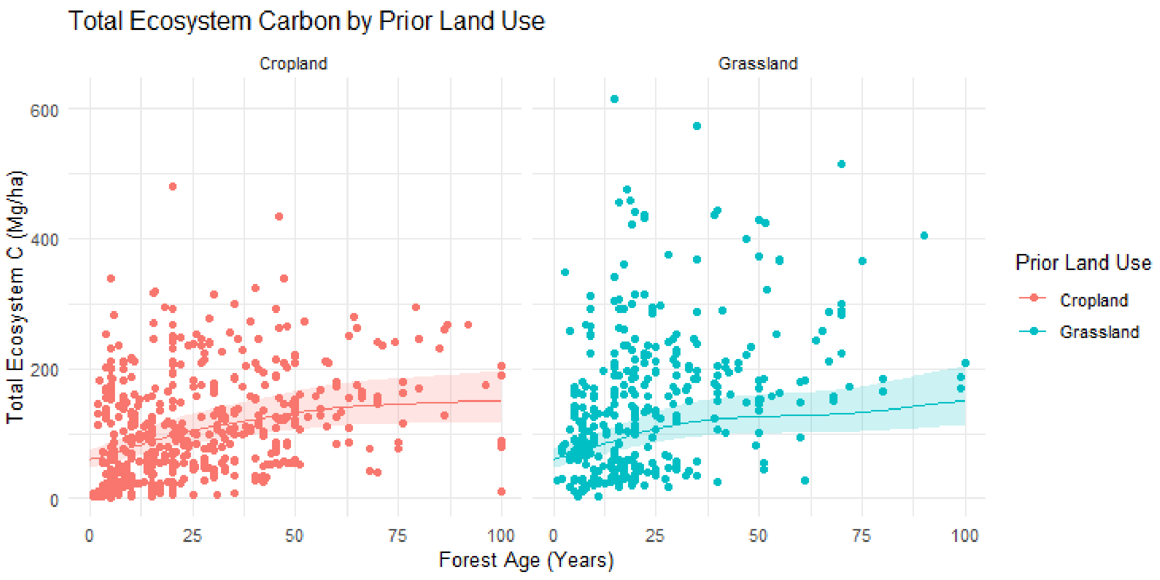


Figure 15. Total ecosystem C over time on sites that were established on prior croplands and grasslands.

4.6 Carbon Accumulation by MAT and MAP

Figure 16 displays the total ecosystem C accumulation using a predictor of 50 years. At lower values of MAP, the MAT has little effect on C accumulation; at higher MAP values, an increase in MAT is correlated with a greater decrease in C accumulation.

Prior literature has reported that AGBC accumulation depends on the interaction between MAT and MAP, with mature forests obtaining the highest AGBC stocks with low MAT (8-10°C) and moderate MAP values (1,000-2,500 mm) (Liu et al., 2014). While our results indicate that the highest total C accumulation occurs with high MAP (>2,000 mm), our study supports high total ecosystem C accumulation at low MAT values.

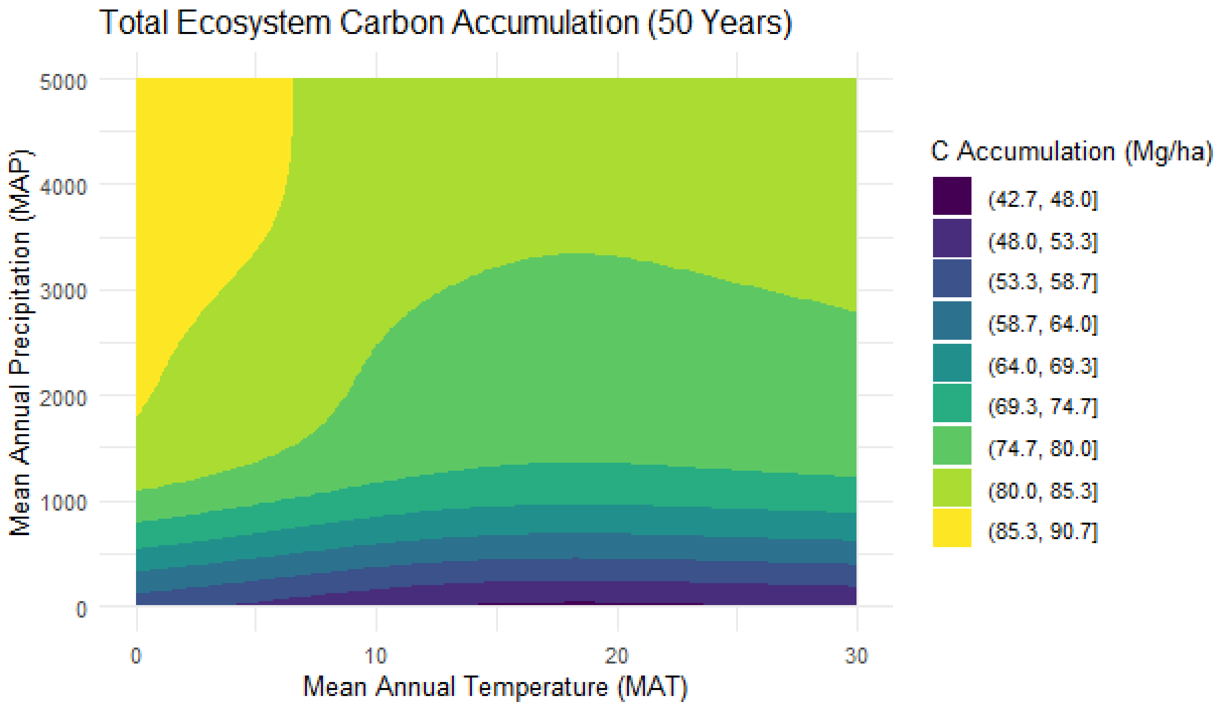


Figure 16. Total ecosystem C accumulation given MAT and MAP. Models were generated given a forest age of 50 years.

Discussion

5.1 Summary of Findings

Though there was high variability in the proportion of C stored in the soil compared to the AGB, we found that there was an overall trend of net positive accumulation in total ecosystem C across time. The accumulation of both SOC and AGBC are highly dependent on forest age, which is consistent with prior literature (Rahlan et al., 2023; Hou et al., 2019; Bukoski et al., 2022; Liu et al., 2018). Additionally, while C accrual occurred most rapidly immediately following forestation, older forests still accumulated C. It has been shown that forests can still accumulate C both aboveground and belowground even on the scale of several centuries (Rahlan et al., 2023), as reaching a steady state with no net C flux may take several hundred years (Liu et al., 2014). While there have been attempts to quantify the upper bound of C sequestration on smaller scales (Smithwick et al., 2002), the maximum C storage potential for forests and the factors affecting maximum C storage (i.e. rising atmospheric carbon dioxide levels or other anthropogenic disturbances) have yet to be explored in depth across regions.

Despite the net positive trend in C accumulation with age, we found that there was a tradeoff between the accumulation of AGBC and SOC dependent on the interaction between forest age and AGBC. The rise in AGBC was associated with lower SOC accumulation, with the impact intensifying in older forests. It is possible that the SOC respiration may increase with higher AGBC due to the priming effect, in which fresh C input from root turnover, root exudates, or tree litter drives soil C decomposition. Root exudates such as oxalic acid may promote the release of soil C from protective mineral associations, increasing its accessibility to soil microbes and driving C mineralization (Keiluweit et al., 2015; Fernandez and Kennedy, 2016). Another possible mechanism of enhanced C decomposition may be the utilization of root exudates by C-limited microbes (Fernandez and Kennedy, 2016). Rhizosphere priming has been shown to be the main mechanism controlling SOM decomposition (Brzostek et al., 2015).

Regarding the impact of mycorrhizal associations on C accumulation, we found that AM forests accumulated the most SOC, leading to greater C accrual on the ecosystem level. Meanwhile, EcM and mixed mycorrhizal forests did not experience significant increases in SOC. These results contribute to the ongoing question within existing literature on the effects of mycorrhizal type on SOC accumulation, particularly regarding EcM trees. Some studies have proposed the existence of the Gadgil effect, in which EcM fungi outcompete free-living microbes for limited resources, limiting their activity and leading to the accumulation of litter stored as SOC (Gadgil and Gadgil, 1971; Wu et al., 2022). Aligning more closely with our results, other studies have proposed that EcM fungi may instead enhance SOC respiration by promoting decomposition to obtain nutrients stored in organic matter or mineral complexes (Frey et al., 2019; Teotia et al., 2017). In contrast, the accumulation of C in AM forests may be due to the high litter production rate of AM trees, which would provide a long-term source of SOC input (Terrer et al., 2021).

On the ecosystem level, plantations and naturally regrowing forests were shown to accumulate similar quantities of C. Although the abundance of total C was similar between both management types, allowing forests to regrow naturally poses additional advantages by enhancing species richness. Forests with higher species richness have demonstrated higher C stability over time in the face of extreme weather events such as droughts (Osuri et al., 2020), and species richness has been shown to positively correlated with total ecosystem C stock and C flux (Liu et al., 2018).

While both prior croplands and grasslands accumulated net positive total ecosystem C and SOC following forestation, croplands accumulated more SOC than grasslands. Regardless of prior land use, plots with low initial SOC accumulated more SOC than those with high initial values. The capability of grasslands to accumulate SOC was surprising, as sites with high initial SOC have previously been shown to lose SOC directly following forestation (Rytter and Rytter, 2020), possibly due to the stimulation of the soil microbial community to respire existing soil C (Fontaine et al., 2007). Meanwhile, the ability for C-depleted cropland soils to act as a C sink has been previously demonstrated in the literature, with croplands even shown to fully recover SOC stocks following conversion to secondary forests (Guo and Gifford, 2002).

5.2 Limitations

This study contains various limitations with regards to data collection and available methods that should be considered when interpreting results. First, most of the studies used in the meta-analysis were conducted using a chronosequence approach, in which plots of varying ages were sampled at the same time. This space-for-time substitution approach assumes that temporal and spatial variation are equivalent, which may not always hold true. For instance, the effects of ecosystem disturbances (e.g. droughts, fires, extreme temperatures), changes in ecosystem dynamics, and resulting transient effects may not be accurately captured or represented (Lal et al., 2005). Additionally, different forest stand locations – even those within the same ecological zone – may exhibit unique environmental conditions leading to variability in results not accounted for by a chronosequence approach (Likens, 1989).

Second, most studies in this meta-analysis contained only SOC field data, with just 30 studies reporting on both SOC stocks and AGB or AGBC stocks. We found that the spatially derived AGBC model used in this study tended to underestimate AGB, particularly in younger forests (< 10 years) that have accumulated less AGB (See Supplementary Fig. 1). The delayed growth response of young trees in the model may contribute to the variability in the percentage of total ecosystem C stored aboveground in earlier stand ages (see Fig. 4). Additionally, this method does not account for the accumulation of C in the dead biomass, which has been shown to accrue C more rapidly than living biomass in middle-aged and older forests (Liu et al., 2014). To account for the C accumulation potential of dead biomass and litterfall and obtain greater accuracy with AGBC estimations, future studies should focus on measuring AGBC in the field in both living and dead biomass along with SOC.

Third, the data distribution is uneven across various combinations of factors such as tree mycorrhizal type and management strategy over time. For instance, while our study contains 267 individual data points for plantations established with EcM species, there are only 63 data points representing EcM forests that have undergone natural regrowth. There is also a current lack of long-term studies of AM forests, as most AM forests in our study are less than 30 years old. Increasing the number of long-term studies would allow for a more reliable prediction of long-term C accumulation under various scenarios.

Although our data displayed an overall trend of net positive ecosystem C accumulation, the long-term stability of C in forests should be considered when implementing forestation efforts as a climate change mitigation strategy. Unlike AGB, which stores C on shorter timescales, soil can store C for several millennia. Still, only a minimal amount of new C may be stabilized in the soil for times longer than the decadal scale (Sierra et al., 2024).

Additionally, forestation may impact global climate through other mechanisms besides C sequestration. Net changes in surface albedo, methane and ozone concentrations, and aerosol scattering following forestation can contribute to a positive radiative forcing effect, which is exacerbated at higher latitudes due to the increased change in albedo from land originally covered in ice and snow (Weber et al., 2024). These effects should be considered when quantifying the effects of forestation on global warming.

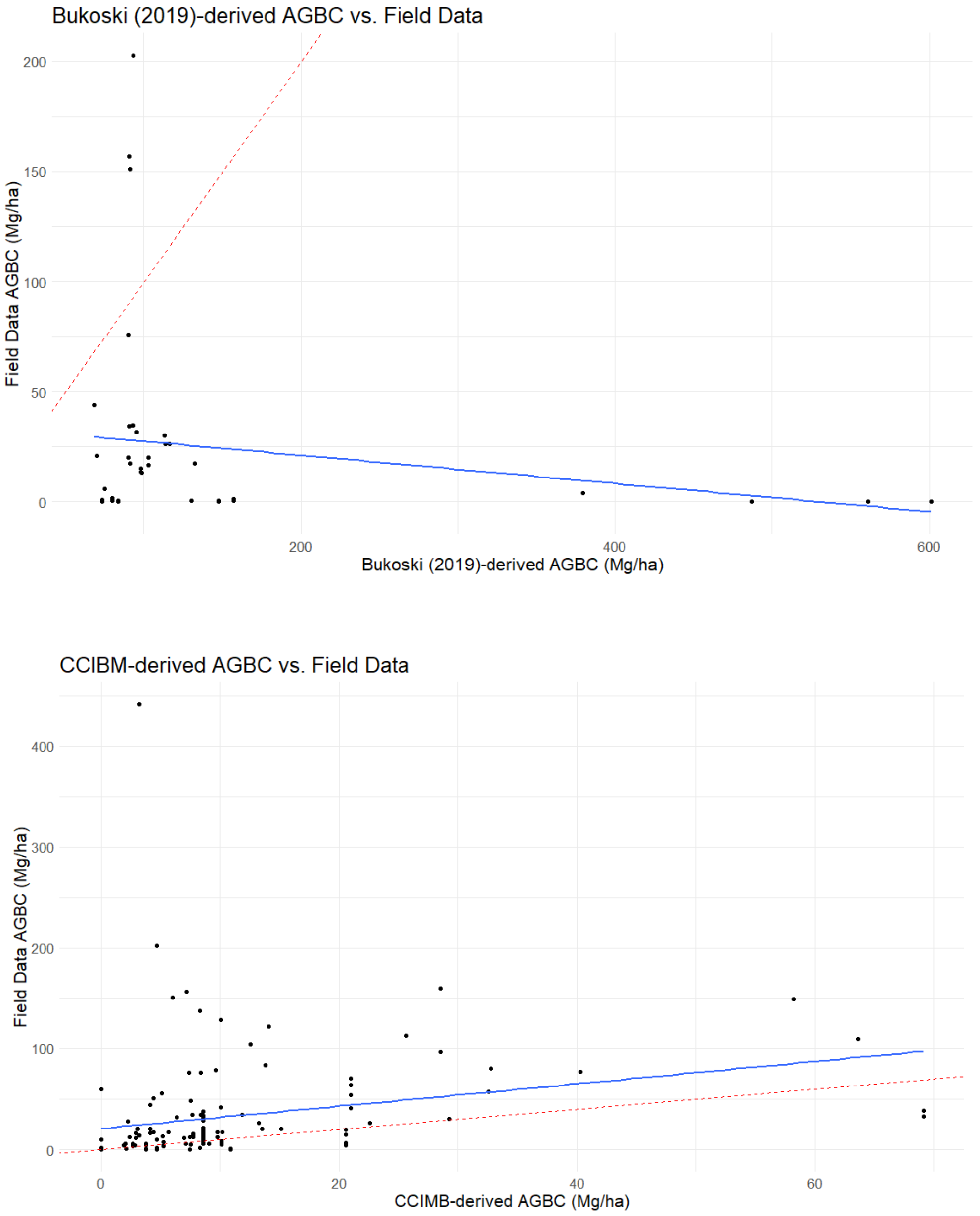
Lastly, future studies on C accumulation would benefit from the standardization of methods, specifically regarding SOC stocks. Studies should consider the spatial distribution of SOC stocks in forests, with SOC stocks being shown to decrease with distance from the tree (Renna et al., 2024). While we standardized SOC stocks to a depth of 60 cm, future research should also aim to standardize the depth of measurement.

Conclusion

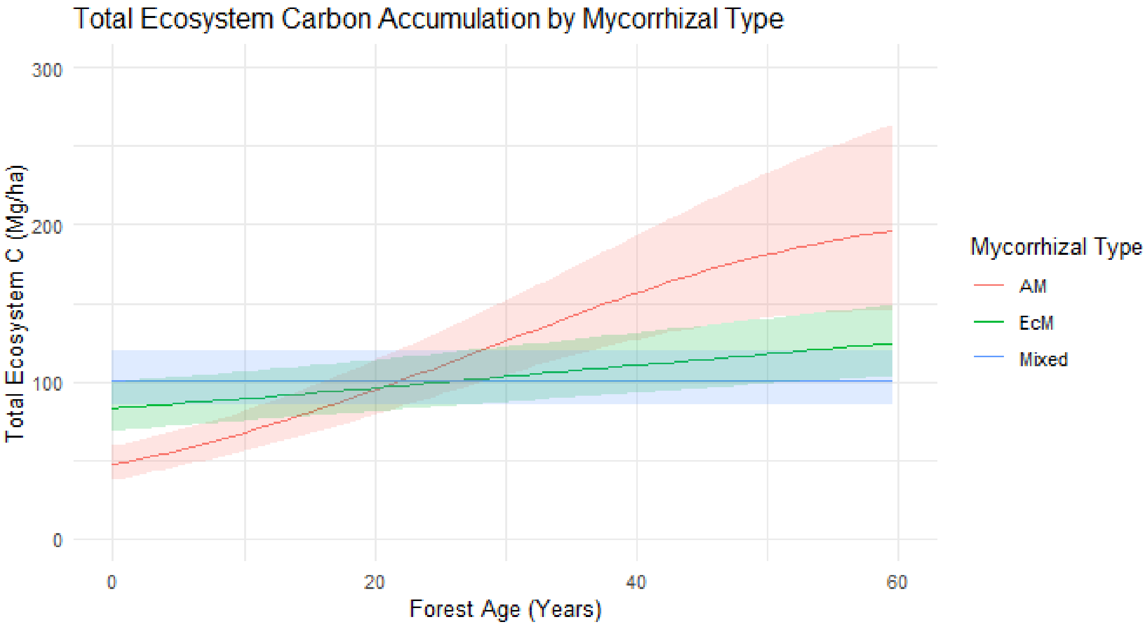
In this thesis, we conducted a global meta-analysis on the factors affecting AGBC versus SOC accumulation following forestation by considering the effects of prior land use, regrowth strategy, mycorrhizal associations, and environmental factors over time. Results indicate that while there is a tradeoff between SOC and AGBC accumulation, the loss of SOC does not negate the increase in AGBC following forestation. Sites with low initial SOC before forest establishment accumulate more soil C than sites with high SOC, regardless of prior land use. Additionally, forests with AM associations accumulate more C over time than both EcM and mixed mycorrhizal forests in the soil and on the ecosystem level.

Despite the potential for forestation to act as a C sink, the use of forestation as a climate change mitigation strategy should be carefully evaluated in the broader political and ecological contexts. The impact of forestation on factors such as biodiversity and long-term food security, and the potential disruption of moving the ecosystem from its natural state (i.e. establishing a forest on a natural grassland) should be considered before implementing forestation projects. Additionally, the use of nature-based solutions such as forestation as an alternative to the direct mitigation of easily abatable C emissions should be avoided (Ellis et al., 2024). However, when implemented properly, forestation offers a natural climate change mitigation method that can contribute to atmospheric carbon dioxide removal and reduce the rate of global warming.

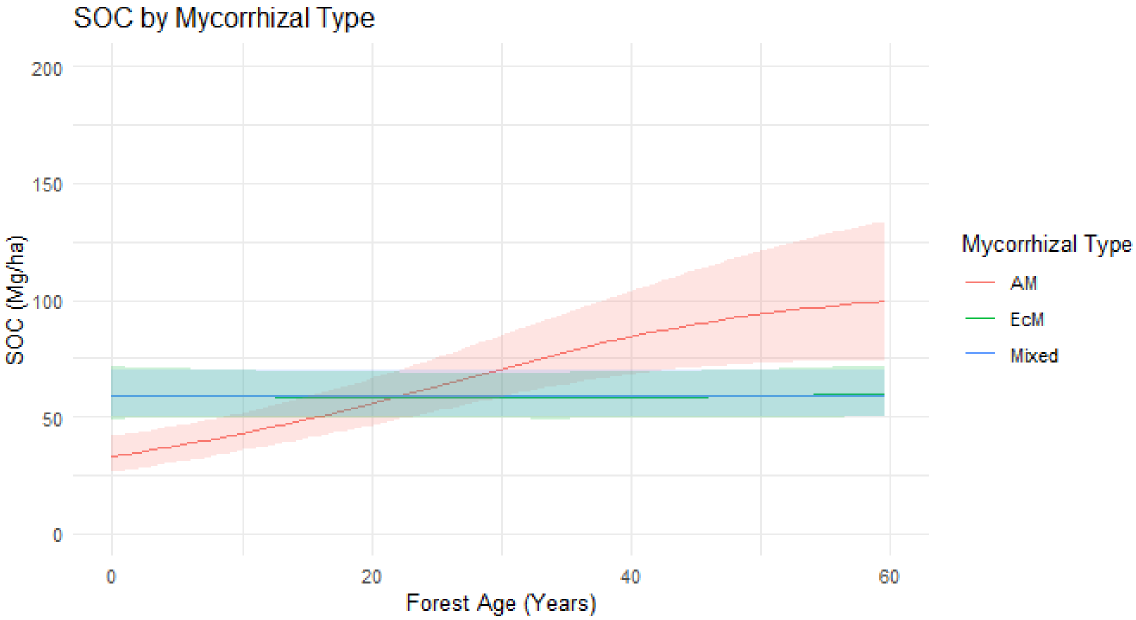
Appendix



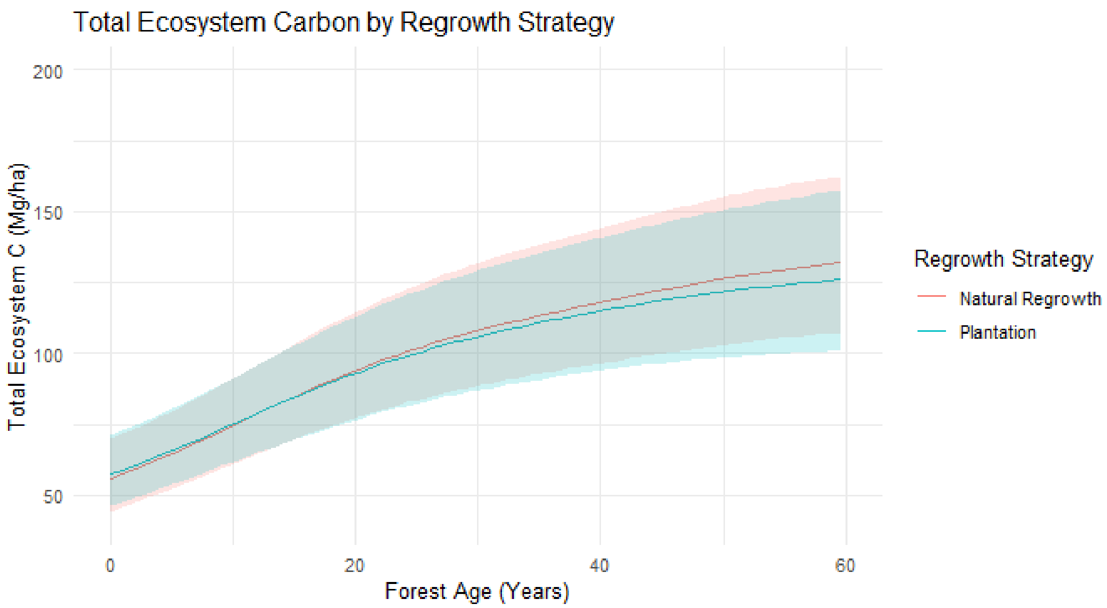
Supplementary Figure 1. Comparison of field-measured AGBC measurements with AGBC derived using parameters from Bukoski et al. (2019) and the CCIBM. Dashed red lines represent a 1:1 ratio between field- and model-derived AGBC values; solid blue lines represent the lines of best fit.



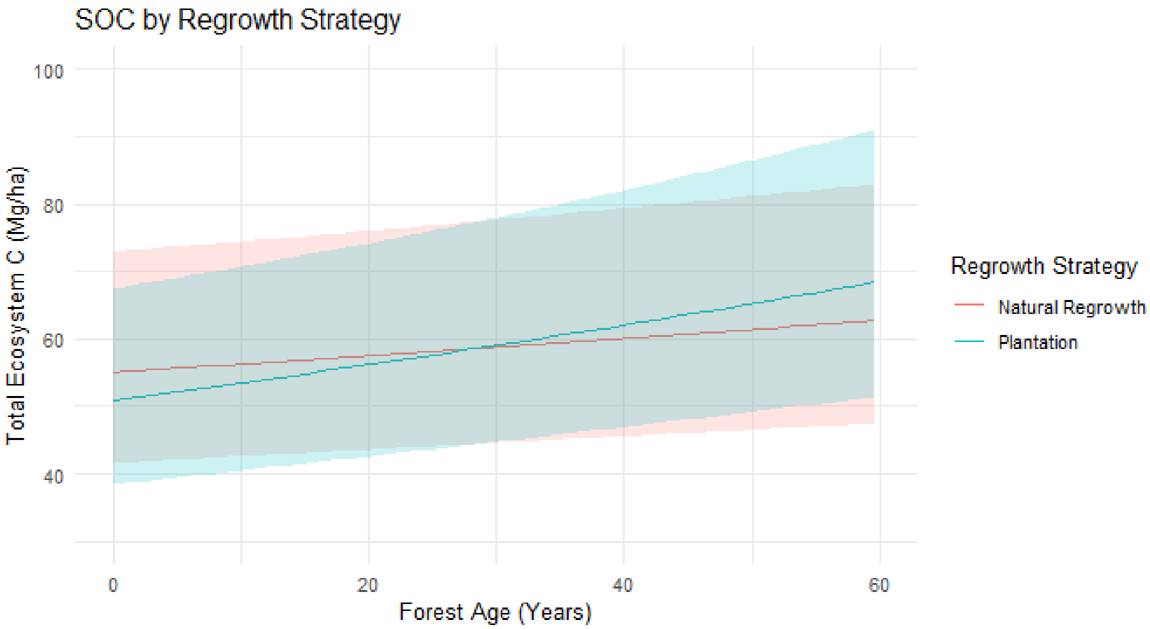
Supplementary Figure 2. Comparison of total ecosystem C over time for AM, EcM, and mixed mycorrhizal associations.



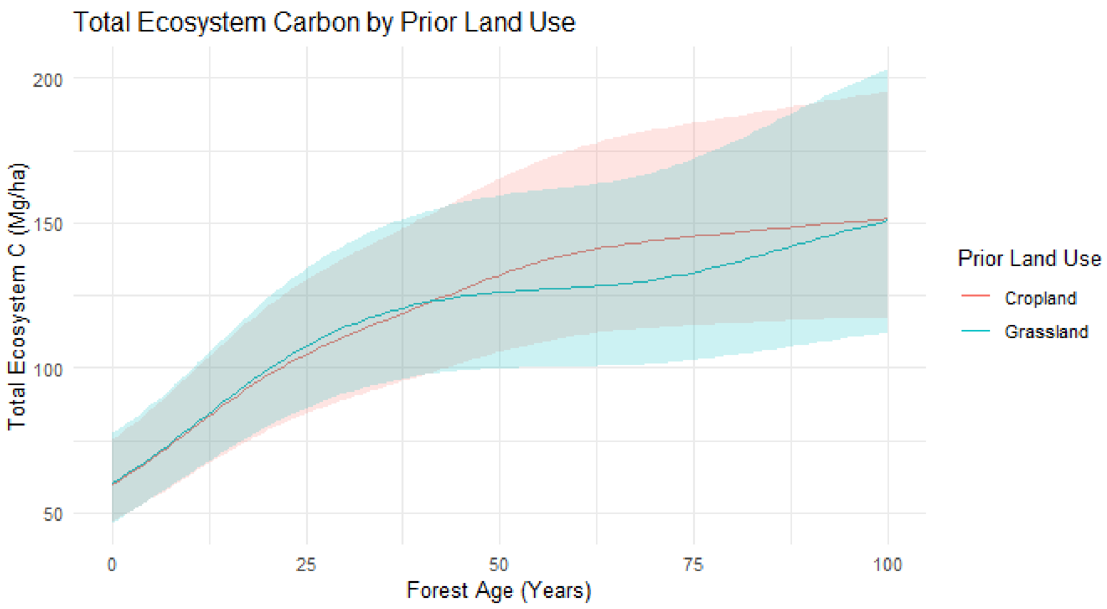
Supplementary Figure 3. Comparison of SOC over time for AM, EcM, and mixed mycorrhizal associations.



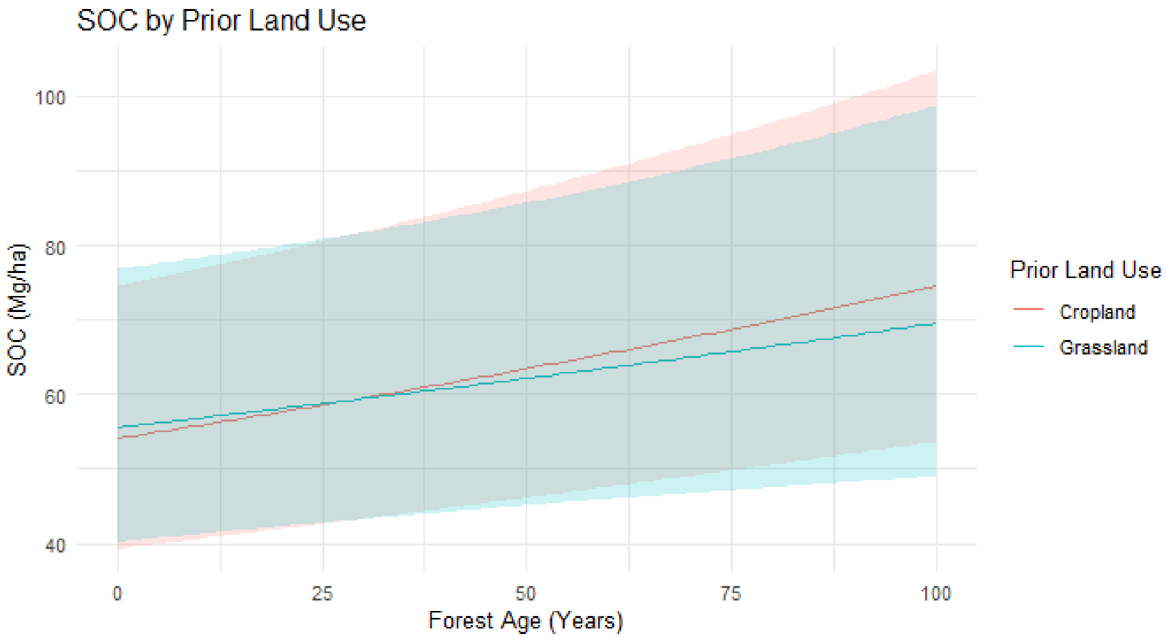
Supplementary Figure 4. Comparison of total ecosystem C over time for sites that underwent natural regrowth and manual planting.



Supplementary Figure 5. Comparison of SOC over time for sites that underwent natural regrowth and manual planting.



Supplementary Figure 6. Comparison of total ecosystem C over time on sites that were established on prior croplands and grasslands.



Supplementary Figure 7. Comparison of SOC over time on sites that were established on prior croplands and grasslands.

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