Effects of Eucalyptus-Castanopsis hystrix Mixed Plantation on Soil Nutrients and Understory Plant Functional Groups: Postprint

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Abstract

The impact of eucalyptus plantations on the ecological environment has long been a subject of global debate, and the ecological effects of mixed eucalyptus and valuable native tree species have attracted considerable attention. To investigate the effects of mixed eucalyptus silvicultural practices on forest soil nutrients and understory plant functional groups, this study used pure eucalyptus stands (PE), eucalyptus × Castanopsis hystrix mixed stands (MEC), and pure C. hystrix stands (PCH) as study objects, and conducted investigations and measurements of understory plant communities and environmental factors. The results revealed that soil physicochemical properties differed significantly among different stand types: soil pH, available nitrogen (AN), and available phosphorus (AP) contents in mixed stands were significantly higher than in pure stands; whereas soil moisture content (SMC), organic carbon (SOC), total nitrogen (TN) contents, and C:N and C:P ratios showed no significant advantage in mixed stands, following a trend of PE > MEC > PCH. Mixed stands significantly increased the species richness of the understory woody plant functional group (WFG), whereas PCH significantly increased the species richness of the fern functional group (FeFG). The importance values of both WFG and the graminoid functional group (GFG) in mixed stands were significantly higher than in pure C. hystrix stands, while the importance value of FeFG in pure C. hystrix stands was significantly higher than in mixed stands. Principal coordinate analysis results showed that the composition of understory plant functional groups did not differ significantly between mixed stands and pure eucalyptus stands, but differed significantly from pure C. hystrix stands. Redundancy analysis revealed that AN and AP were the main influencing factors for WFG dominance, SMC, TN, and SOC were the main influencing factors for FeFG dominance, and SBD was the main influencing factor for GFG dominance. The results indicate that in southern subtropical regions, mixing eucalyptus with

C. hystrix can, to a certain extent, improve forest soil nutrient availability and understory plant diversity.

Full Text

Preamble

Effects of a mixture of Eucalyptus and Castanopsis hystrix on soil nutrients and understory plant functional groups

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Abstract: The impact of Eucalyptus plantations on the ecological environment has been a hot topic of controversy worldwide. The ecological and environmental effects of a mixture of Eucalyptus and precious native tree species have attracted much attention. In order to explore the effects of management measures in mixed plantations on soil nutrients and understory plant functional groups, we assessed the understory plant communities and environmental factors using pure Eucalyptus plantations (PE), mixed Eucalyptus and Castanopsis hystrix plantations (MEC), and pure C. hystrix plantations (PCH). We found significant differences in the physicochemical properties of soil in the different stands. The soil pH, available nitrogen (AN) content, and available phosphorus (AP) content were significantly higher in MEC than in PE and PCH. However, we noted no significant advantages in terms of the soil moisture content (SMC), soil organic carbon (SOC) content, total nitrogen (TN) content, C:N ratio, and C:P ratio in MEC, with a trend of PE $<$ MEC $<$ PCH. On the other hand, the soil bulk density (SBD) and total phosphorus (TP) content showed a trend of PE $>$ MEC $>$ PCH. MEC significantly increased the species richness of the understory woody functional group (WFG), while PCH significantly increased the species richness of the ferns functional group (FeFG). The importance value of WFG and the Gramineae functional group (GFG) was significantly higher in MEC than in PCH, while the importance value of FeFG was significantly higher in PCH than in MEC. Principal coordinate analysis revealed no significant difference in the composition of understory plant functional groups between MEC and PE but revealed a significant difference between MEC and PCH. Moreover, redundancy analysis revealed that AN and AP were the main factors influencing the dominance of WFG. SMC, TN content, and SOC content were the main factors influencing the dominance of FeFG, while SBD was the main factor influencing the dominance of GFG. Thus, the mixture of Eucalyptus and C. hystrix could improve the availability of soil nutrients and the diversity of understory

plant communities to some extent in subtropical China.

Key words: Mixed Eucalyptus and C. hystrix plantations, soil nutrient, plant diversity, species richness, plant functional group

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1.1 Study Area Description

The study area is located in the Qingshan Experimental Forest Farm of the Tropical Forestry Experimental Center, Chinese Academy of Forestry, in Pingxiang City, Guangxi (21°57' 47" ~22°19' 27" N, 106°39' 50" ~106°59' 30" E). The experimental site is characterized by low hills with elevations ranging from 130 to 1,045.9 m and complex topography. The soil is primarily laterite derived from granite weathering. The region has a south subtropical monsoon climate, with an extreme minimum temperature of -1.5°C, an extreme maximum temperature of 40.3°C, and a mean annual temperature of 20.5–21.7°C. Annual precipitation ranges from 1,200 to 1,500 mm, with distinct wet and dry seasons (April–September being the rainy season). Annual evaporation is 1,261–1,388 mm, and relative humidity is 80–84%.

The original vegetation at the experimental site was a 35-year-old Pinus massoniana plantation. After harvesting in February 2012, the site was prepared by slash burning and hole planting to establish pure and mixed plantations of Eucalyptus and C. hystrix. All stands were planted with alternating narrow and wide rows: narrow row spacing was 2 m, wide row spacing was 7 m, and within-row spacing was 2 m for all rows [Figure 1: see original paper]. Pure plantations had a density of 1,333 trees $\cdot$ hm^{-2}. In mixed plantations, Eucalyptus was planted in narrow rows at a density of 1,333 trees $\cdot$ hm^{-2}, while C. hystrix was planted between wide rows at 2 m spacing, resulting in 334 trees $\cdot$ hm^{-2} and a mixing ratio of 8:2. All stands were prepared by manual strip tillage (1 m wide, 20 cm deep) before planting. Planting holes measuring 50 cm × 50 cm × 30 cm were dug manually, and 250 g of compound fertilizer was applied as base fertilizer per hole 7 days before planting. Manual weeding was conducted in autumn 2012 and 2013.

1.2 Sample Plot Establishment and Understory Plant Community Survey

This study focused on two tree species: C. hystrix and Eucalyptus. In May 2019, we selected typical south-facing slopes with consistent site conditions in pure Eucalyptus plantations (PE), mixed Eucalyptus and C. hystrix plantations (MEC), and pure C. hystrix plantations (PCH). Five 20 m × 20 m survey plots were randomly established in each stand type, totaling 15 plots . Each 20 m × 20 m plot was subdivided into four 10 m × 10 m subplots for tree layer investigation, where tree density, diameter at breast height (DBH), height, clear bole height, and crown width were recorded. Within each subplot, a 5 m × 5 m quadrat was established for understory vegetation survey, recording species names, individual counts, height, and coverage.

1.3 Soil Sample Collection and Measurement

In each plot, nine random sampling points were selected. Soil bulk density was measured at 0–20 cm depth using the ring knife method. Soil samples from 0–20 cm depth were collected using a stainless steel auger (8.5 cm inner diameter). After removing plant roots and gravel, samples were mixed thoroughly and passed through a 2 mm sieve. Each sample was divided into two portions: one air-dried for physicochemical analysis and another stored at 4°C for ammonium and nitrate nitrogen determination.

Soil bulk density (SBD) was measured using the ring knife method, soil moisture content (SMC) by the oven-drying method, and soil pH using a pH meter (Starter 2100, Ohaus, USA) at a soil:water ratio of 1:2.5 (w/v). Soil organic carbon (SOC) was determined by the $K_2Cr_2O_7$-H_2SO_4 external heating method. Total nitrogen (TN) and available nitrogen (AN) (ammonium and nitrate nitrogen) were measured using a continuous flow analyzer (AA3, Bran Luebbe). Total phosphorus (TP) was determined by H_2SO_4-$HClO_4$-molybdenum antimony colorimetry, and available phosphorus (AP) by double acid (HCl-H_2SO_4) extraction-molybdenum antimony colorimetry (Bao, 2000).

1.4 Data Analysis

Following Miller & Chamberlain (2008), understory vegetation was classified into five plant functional groups: woody plant functional group (WFG), vine functional group (VFG), gramineae plant functional group (GFG), fern functional group (FeFG), and forb functional group (FoFG). The importance value (IV) of each understory plant species was calculated to characterize its status and dominance in the community (Gilliam, 2007):

$$IV = 100 \times (Ra + Rp + Rc)/3$$

where Ra is relative abundance (percentage of individuals of a species relative to total individuals), Rp is relative frequency (percentage of quadrats where a species occurs), and Rc is relative coverage (percentage of coverage of a species).

One-way ANOVA in SPSS 24.0 for Windows was used to test significant differences in soil nutrients, functional group species richness, and importance values among stands, with LSD multiple comparisons at $P < 0.05$. Principal coordinate analysis (PCoA) was used to examine differences in understory plant functional group composition among the three stand types. Redundancy analysis (RDA) was performed with stand factors (canopy density, basal area) and measured soil physicochemical factors as explanatory variables to identify main factors influencing understory plant functional group variation and their explanatory power. PCoA and RDA were conducted using the vegan package in R 3.5.1.

2.1 Soil C, N, P and Their Stoichiometric Ratios

Soil moisture content in PCH [(37.47 ± 4.45)%] was significantly higher than in PE and MEC, with no significant difference between PE and MEC. Soil bulk density in MEC was intermediate between PE and PCH, with no significant differences among them. However, SBD in PE [(1.33 ± 0.07) $g \cdot cm^{-3}$] was 8.27% higher than in PCH [(1.22 ± 0.08) $g \cdot cm^{-3}$], a significant difference. Soil pH, AN content, and AP content in MEC were significantly higher than in PE and PCH. Specifically, soil pH in MEC (5.00 ± 0.13) was 11.8% and 9% higher than in PE (4.41 ± 0.07) and PCH (4.55 ± 0.10), respectively. AN content in MEC [(21.56 ± 1.81) $mg \cdot kg^{-1}$] was 17.49% and 16.60% higher than in PE [(17.79 ± 1.02) $mg \cdot kg^{-1}$] and PCH [(17.98 ± 1.28) $mg \cdot kg^{-1}$], respectively. AP content in MEC [(8.00 ± 0.38) $mg \cdot kg^{-1}$] was 43.88% higher than in PE [(4.49 ± 0.24) $mg \cdot kg^{-1}$], while AP in PE was 15.28% lower than in PCH [(5.30 ± 0.58) $mg \cdot kg^{-1}$] .

Analysis revealed significant differences in soil organic carbon among stands, with the ranking PCH > MEC > PE, though differences in soil total phosphorus content were not significant. Total nitrogen content was highest in PCH, significantly different from PE, while TN in MEC was intermediate with no significant differences from PE or PCH. Significant differences were found in soil C:N and C:P ratios among stands, while N:P ratio was highest in PCH and significantly different from PE; MEC was intermediate with no significant differences from PE or PCH [Figure 2: see original paper].

2.2 Understory Plant Species and Functional Group Composition

Different management modes significantly affected understory plant species composition and importance values. A total of 112 vascular plant species belonging to 47 families and 97 genera were recorded. MEC had the most species (73), followed by PE (61), and PCH had the fewest (59) . The dominant species composition of understory plant communities varied significantly among stands .

One-way ANOVA showed that species richness of WFG in MEC was significantly higher than in PE and PCH, and PE was significantly higher than PCH ($P < 0.05$). No significant differences were found in species richness of VFG, GFG, or FoFG among stands ($P > 0.05$). Species richness of FeFG in PCH was significantly higher than in PE and MEC ($P < 0.05$), with no significant difference between PE and MEC ($P > 0.05$).

Stand type significantly affected the importance value of WFG ($P < 0.05$). The importance value of WFG in MEC and PE was significantly higher than in PCH, with no significant difference between MEC and PE ($P > 0.05$). No significant differences were found in importance values of VFG among stands ($P > 0.05$). The importance value of GFG in PCH was significantly lower than in PE and

MEC ($P < 0.05$), with no significant difference between PE and MEC ($P > 0.05$). The importance value of FeFG in PCH was significantly higher than in PE and MEC ($P < 0.05$), with no significant difference between MEC and PE ($P > 0.05$). No significant difference was found in importance values of FoFG between PE and MEC ($P > 0.05$) [Figure 3: see original paper].

Principal coordinate analysis (PCoA) of understory plant functional group composition showed that the first two axes explained 91.54% of the total variation. Axis 2 clearly separated PCH from PE and MEC, indicating differences in plant functional group composition between PCH and the other stand types. In contrast, PE and MEC could not be separated by any principal component axis, suggesting similar species composition of understory plant functional groups [Figure 4: see original paper]. Permutational multivariate analysis of variance also revealed significant differences in species composition of understory plant functional groups between PCH and PE (or MEC), but no significant difference between PE and MEC .

2.3 Factors Influencing Understory Plant Functional Group Composition

Redundancy analysis (RDA) showed that the first and second principal component axes explained 58.6% and 6.3% of the variation in understory plant functional group composition, respectively [Figure 5: see original paper]. WFG was significantly correlated with AP and AN, which were the main factors influencing WFG dominance. FeFG was significantly correlated with SOC, TN, and SMC, which were the main factors influencing FeFG dominance. SBD was the main factor influencing GFG dominance.

Species diversity reflects the comprehensive expression of species richness and distribution uniformity, representing stand structure, organization level, development stage, stability, and habitat differences (Ma, 2013). Compared with natural forests, plantation composition and structure are relatively simple, typically exhibiting lower understory biodiversity and poorer ecosystem stability. Studies have shown that in Eucalyptus plantations under successive short-rotation regimes, understory vegetation is dominated by native woody plants in the first 1–2 rotations, shifts to native herbaceous plants by the 3rd–4th rotations, and becomes dominated by exotic invasive plants by the 5th–6th rotations, leading to severe degradation of understory plant functional groups (Zhou et al., 2020). Some scholars attribute the decline in stability and biodiversity of Eucalyptus plantations to large-scale contiguous planting (Chen, 2001). Mixing is a common silvicultural practice that optimizes stand structure by altering density and species composition, promoting material cycling, improving soil properties, and enhancing understory species diversity (Chen et al., 2017; Ratcliffe et al., 2015; Sun et al., 2015). Consequently, mixed forests tend to be more stable than pure plantations (Yan et al., 2020). Our results demonstrate that mixing Eucalyptus with C. hystrix significantly increased understory species richness, particularly for woody plants, with 36 species in mixed stands—significantly more than the

31 species in pure Eucalyptus and 27 in pure C. hystrix stands–consistent with findings from other studies (Pang et al., 2020; Yang, 2007; Berger & Puettmann, 2000).

Understory shrub layers play a crucial role in maintaining species diversity and healthy, stable forest community structure (Zhang et al., 2019). For instance, understory woody plants in Eucalyptus plantations positively affect soil microenvironment improvement and nutrient availability maintenance, representing key factors for sustaining soil ecosystem multifunctionality (Zhou, 2016). Forest canopy structure and resulting light environment directly or indirectly influence understory plant composition and diversity (Ou & Su, 2012), particularly in maintaining and shaping shrub layer diversity (Yan et al., 2020). In this study, the multi-layered structure formed by mixing Eucalyptus and C. hystrix significantly increased WFG species richness but did not significantly affect VFG, GFG, FeFG, or FoFG richness, suggesting that the moderate canopy density created by the horizontal and vertical structure of mixed stands may favor WFG establishment. Additionally, light conditions are important environmental factors affecting dominant species composition and diversity (Pang et al., 2018). For example, thinning in Chinese fir plantations altered light, temperature, and moisture conditions, significantly increasing or decreasing understory species richness and changing functional group composition (Li et al., 2020). Among our three stand types, PCH had the highest canopy density but lowest overall species richness, yet its FeFG richness was significantly higher than in PE and MEC. This may be because PCH' s high density, low tree height, and long, full crowns create a shaded environment favorable for shade-tolerant ferns to colonize and become dominant.

Plant functional groups are classified based on differences in plant physiological morphology, life history, or other functional attributes related to ecosystem functioning (Fan et al., 2016). In grassland ecosystems, plants adapt to complex environments through functional group reorganization (Li et al., 2015). In forest ecosystems, habitat factors are closely related to understory plant functional group composition; for instance, changes in canopy structure are major drivers of understory functional group variation (You et al., 2018). Our study found that in PE with tall trees and low canopy density, WFG and GFG were dominant, with importance values ranking WFG > GFG > VFG > FeFG > FoFG. In MEC with a two-layered structure and moderate canopy density, the ranking was WFG > GFG > FeFG > VFG > FoFG, with WFG and GFG remaining dominant. In PCH with the shortest trees and highest canopy density, the ranking became FeFG > WFG > VFG > GFG > FoFG, with ferns becoming dominant. Community species composition and individual distribution result from species interactions and environmental disturbances (Mao & Zhu, 2006; Buckley et al., 2003; Sagar et al., 2003). Plant diversity is closely related to habitat conditions, and when these conditions change, communities succeed in different directions, altering system structure and function (Wang et al., 2001). Our PCoA and multivariate analysis showed similar understory functional group composition between PE and MEC but significant differences between PCH and the other two stands, with 91.54% of variation explained. Since pre-planting habitat conditions and management measures were consistent across stands, differences in functional group composition likely resulted from interspecific competition and adaptation in the heterogeneous environments that developed later, reflecting natural principles of species coexistence and survival of the fittest.

Soil in forest ecosystems serves as a crucial site for material cycling and energy conversion, a carrier for plant community succession, and a key environmental factor influencing plant community distribution (Li et al., 2012; Geng et al., 1999). Soil physicochemical properties are closely related to plant community composition and diversity (Zhou, 2016; Siefert et al., 2012). Our study found that MEC, with the highest understory species richness, also had significantly higher soil AN, AP, and pH than PE and PCH with lower richness. Mixed forests can fully utilize above- and below-ground space and resources (Sagar et al., 2003; Wang et al., 2001), increase litter quantity and quality, promote nutrient return, and improve nutrient availability and utilization, thereby affecting plant diversity (Li et al., 2012; Geng et al., 1999).

Soil fertility, moisture, and texture significantly affect plant community distribution (Siefert et al., 2012), and vice versa. For example, removing understory woody plants in Eucalyptus plantations significantly reduced soil nutrient availability, while removing herbaceous and fern functional groups increased it (Zhou, 2016), indicating complex interdependence between functional group traits and soil fertility. Our results show that AP and AN are key factors for WFG dominance, SOC, TN, and SMC drive FeFG dominance, and SBD influences GFG dominance.

However, environmental factors affecting vegetation growth and distribution are complex. Some studies found significant correlations between soil phosphorus content and plant community diversity (Gartlan et al., 1986), suggesting phosphorus use efficiency may affect plant distribution (Yan et al., 2019). In Chinese fir plantations, soil total and available potassium significantly affected FoFG variation, while total phosphorus and N:P ratio significantly affected GFG variation (Li et al., 2020). These findings partially align with ours, reflecting heterogeneity in forest ecosystem composition, structure, and spatiotemporal scales. Other soil factors showed non-significant effects, possibly due to small differences among stands or the temporal scale of stand development.

In summary, different silvicultural modes significantly affected soil physicochemical properties, understory plant species composition, and importance values in south subtropical regions. Compared with pure Eucalyptus and C. hystrix plantations, mixing Eucalyptus with C. hystrix for seven years significantly increased understory species richness, particularly WFG richness, and significantly improved soil pH, AN, and AP content, enhancing soil nutrient availability. Soil physicochemical properties significantly influenced understory functional group distribution: TN and TP were key factors for WFG dominance; SMC, TN, and SOC drove FeFG dominance; and SBD influenced GFG dominance. However, plant community composition and structural diversity dynamics in forest ecosystems involve complex spatiotemporal processes. Understanding the effects of silvicultural practices on understory functional groups and soil quality requires long-term monitoring and continuous research. This study provides preliminary results from 7-year-old pure and mixed plantations, and further research is needed to elucidate the underlying mechanisms.

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Note: Figure translations are in progress. See original paper for figures.