Austrian Journal of Forest Science

Centralblatt für das gesamte Forstwesen

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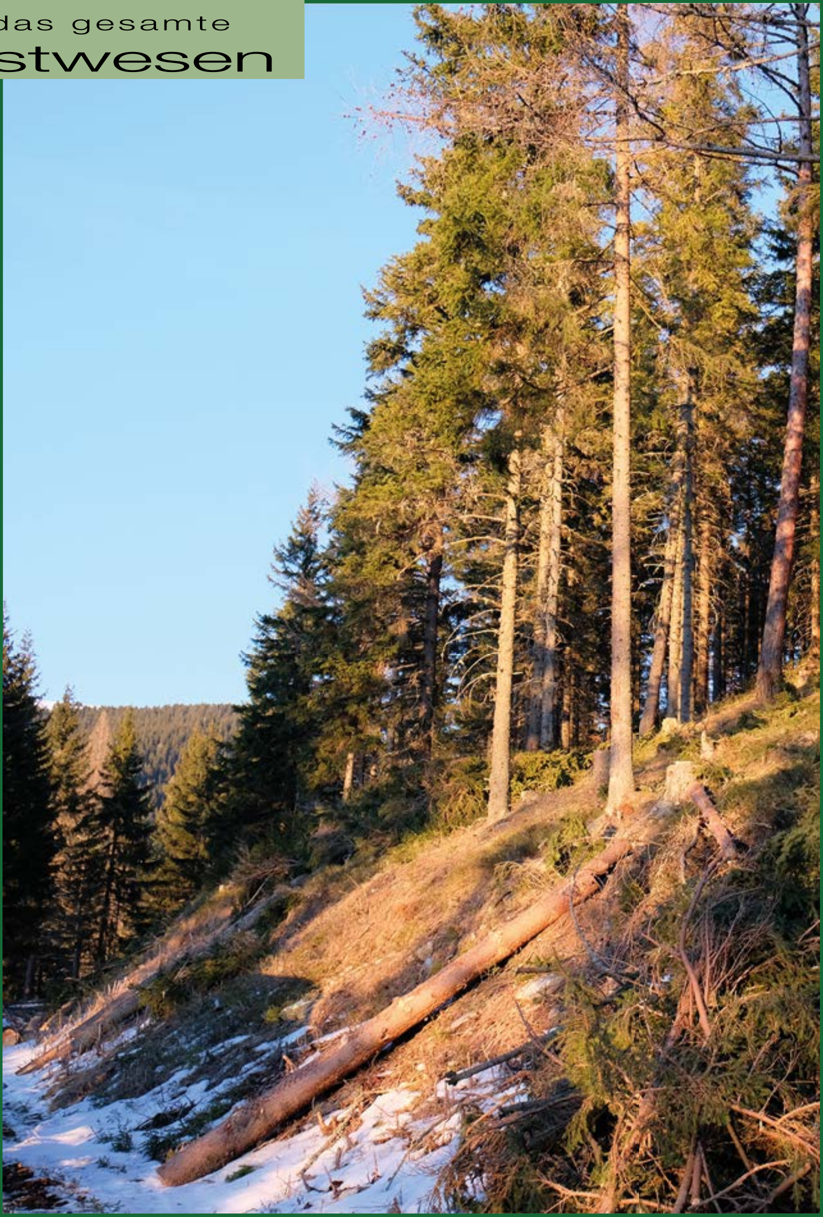

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Soil properties and understory species diversity at different stand densities in a tropical rainforest on Hainan Island, China

Bodeneigenschaften und Artenvielfalt bei unterschiedlicher Bestandsdichte in einem tropischen Regenwald auf der Insel Hainan, China

Benxue Chen[1,2†], Yanbing Li[1†], Shaohui Fan[2], Chao Peng[3], Biao Huang[2], Guanglu Liu[2*]

Keywords: Shrub, liana, interlayer plants, herbs, Soil properties, Diversity, RDA analysis, Secondary forests, management, restoration

Schlüsselbegriffe: Büsche, Lianen, Krautschicht, Bodeneigenschaften, Vielfalt, RDA Analyse, Sekundärwälder, Management, Wiederherstellung

Abstract

Stand density has obvious effects on understory vegetation – an important part of forest ecosystems. Understory biodiversity in tropical rainforests is important for the natural regeneration potential, which is critical for improving the overall function of forest ecosystem. We investigated the effects on plant species diversity (separated in shrubs, interlayer plants and herbs) and soil physical and chemical properties at five levels of stand density (5000, 6500, 8000, 9500, and 11000 trees·ha^{-1}) in tropical rainforests on the Hainan Island, China. The results showed that soil water content increased with stand density, while organic matter content and both total and available phosphorus content was highest in the moderately dense stand. There was no effect of stand density on the diversity of interlayer plant species (climbing vines). The diversity of the interlayer was consistently greater than herbs, especially at high stand

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density. Diversity of herbs was lowest in the high-density stand (11000 trees·ha^{-1}). Species richness and Simpson's index of dominance of the shrub layer and species richness and its Shannon-Wiener diversity index of the herb layer were both highest at moderate stand density (8000 trees·ha^{-1}). Species richness and Shannon-Wiener diversity index of interlayer plants peaked at higher stand density (9500 trees·ha^{-1}), and the Simpson dominance index generally increased with stand density, indicating that climbers are more competitive in denser tropical rainforests. Stand density influenced the diversity and composition of understory species. We found positive correlations for understory plant species diversity with soil water content, organic matter content, total phosphorus, and available phosphorus content. Our results indicate that moderate stand densities of 8000–9500 trees·ha^{-1} seem optimal for enhancing understory species diversity, soil fertility, stand stability, and natural regeneration. It could be used as target density for managing secondary tropical lowland rainforests.

Zusammenfassung

Die Bestandesdichte beeinflusst die Bodenvegetation, die ein wichtiger Teil von Walddökosystemen ist. Die Biodiversität der Bodenvegetation in tropischen Regenwäldern ist wichtig für die Naturverjüngung, die wiederum entscheidend ist für die Erhaltung und Verbesserung der Waldfunktionen. Wir untersuchten die Diversität (unterteilt in Sträucher, Lianen/Inter-layer Pflanzen und krautige Vegetation) und die geochemischen Bodeneigenschaften unter fünf verschiedenen Bestandesdichten (5000, 6500, 8000, 9500 und 11000 Bäume pro Hektar) in einem sekundären tropischen Tieflandregenwald auf der Insel Hainan, China. Unsere Ergebnisse zeigten, dass der Bodenwassergehalt mit Bestandesdichte steigt, während der Gehalt an organischer Substanz und der Phosphourgehalt im Boden am höchsten bei mittlerer Bestandesdichte war. Die Bestandesdichte hatte keinen klaren Einfluss auf die Diversität in Lianen, dafür war die Diversität der Krautschicht am größten bei hoher Bestandesdichte (11000 ha^{-1}). Artenanzahl und Simpson Index der Strauchschicht sowie Artenanzahl und Shannon-Wiener Index der Krautschicht waren am höchsten bei mittlerer Bestandesdichte (8000 ha^{-1}). Bei den Lianen waren Artenanzahl und Diversitätsindices am höchsten unter der zweithöchsten Bestandesdichte (9500 ha^{-1}), was vermuten lässt, dass Kletterpflanzen konkurrenzstärker bei mittlerer Bestandesdichte sind. Wir konnten positive Zusammenhänge zwischen Biodiversität und Bodenwassergehalt, Organikanteil, Gesamt Phosphour und verfügbaren Phosphour feststellen. Die Bestandesdichte beeinflusst somit die Diversität und Zusammensetzung der Bodenvegetation auf unterschiedliche Weise. Mittlere Bestandesdichte von 8000-9500 ha^{-1} erscheint optimal für hohe Biodiversität in der Bodenschicht, Nährstoffversorgung, Bestandesstabilität und natürliche Verjüngung. Dies kann als Zielstammzahl für das Management von sekundären tropischen Tieflandregenwäldern verwendet werden.

1. Introduction

Species diversity is one of the most important characteristics in plant communities, reflecting species richness and the stability and dynamics of a community (Hu, 2016). Diversity indexes are comparable indicators for species richness, productivity, stability and ecological functioning of forest communities at the level of individual plants (Ahmad, 2018). Soil is the basis for plants roots and growth and in consequence their occurrence and development within the community. Fertile soil can improve the uptake of water and nutrients, and thus directly or indirectly affect the growth of plants (Castello, 2011; Wingfield, 2015). On other hand, the growth of plants, their properties and abundance can also cause changes to soil physical and chemical properties, thereby affecting soil stability and plant growth (Pohl, 2009).

Stand density is the number of standing live trees per unit area, which is a useful factor for evaluating forest productivity, as it is linked to tree growth (Luo, 2010). Differences in stand density can result in large variations in the environmental condition of the understory, leading to remarkable difference of growth in all vegetation layers (Lu, 2007). If the stand density is too high, the conditions for the understory is poor, which could restrict growth and lower species diversity. On the other hand, at too low density a few highly competitive species will likely gain superiority, which limits the balanced coexistence of more species and makes it difficult to maintain the level of species diversity. We hypothesize that at moderate density many species have their greatest chance of survival (Zhang, 2019).

Since stand density influences environmental conditions, such as light, heat, and water, it drives changes in the upper canopy as well as understory species richness and diversity (Nguyen, 2014; Bam, 2010). As the forest canopy density increases, the transmittance of the canopy decreases, and the growth and development of undergrowth vegetation are inhibited (Liu, 2014), thus causing changes to species diversity (Wang, 2020). From a forest management perspective, using an appropriate stand density is critical to maintaining species diversity and soil nutrient cycling (Ares, 2010; Xu, 2019).

Tropical rainforests are riche in species diversity and conservation value and among the structurally most complex terrestrial ecosystems, playing an important role in maintaining the global carbon cycle, protecting biodiversity, and regulating climate (Gentry, 1982). Due to environmental change and human disturbance, the area and quality of tropical rainforests have decreased considerably worldwide (Liu, 2018). There are many studies of tropical rain forests, mostly focusing on the impacts of canopy gaps (Li, 2019; Devagiri, 2016), selective logging (Berry, 2008; Brown, 2004), and soil seed banks on species diversity or vegetation types (Olano, 2002). We are not aware of studies focusing on understory species diversity and soil physical and chemical properties of tropical rainforest across stands of different tree densities.

In this study, we investigated the effects of five levels of stand densities on understory species diversity and soil physical and chemical properties, and their correlations for the tropical rainforest on Hainan Island. Determining the optimal stand density could help protect the biodiversity of tropical rainforest and improve forest quality.

2. Material and Methods

2.1 Study sites

The study area is located in Ganzaling, Hainan Province, China (18°20'–18°21'N, 109°34'–109°42'E; *Fig. 1*), at elevations ranging from 200 to 350 m. The region has a tropical oceanic monsoon climate, with abundant rainfall and sunshine, and moderate temperatures. The mean annual temperature is 25.4 °C, the solar period is 2563 hours and the annual rainfall is about 2200 mm. The bedrock is granite with mainly acid red soils. The study area is dominated by secondary forests with minimal intervention. Dominant canopy tree species are H*opea reticulate, Acronychia pedunculata, Croton laevigatus, Pterospermum acerifolium, Vatica mangachapoi,* and *Microcos paniculata*. The shrub layer is dominated by *Psychotria rubra, Wikstroemia liangii, Glochidion zeylanicum, Memecylon nigrescens,* and *Licuala fordiana*. The dominant interlayer plant are *Entada phaseoloides, Rattan, Uvaria calamistrata, Ancistrocladus tectorius, Toxocarpus patens,* and *Coelospermum kanehirae*. The dominant herbs are *Aspidistra elatior, Scleria terrestris,* and *Alpinia oxyphylla*. Fig. 2 provides overview of the considered layers. The study area is located in a nature reserve and the stands developed through natural regeneration after large-scale deforestation in the 1980s. Aside of that, here are no other records of human disturbance.

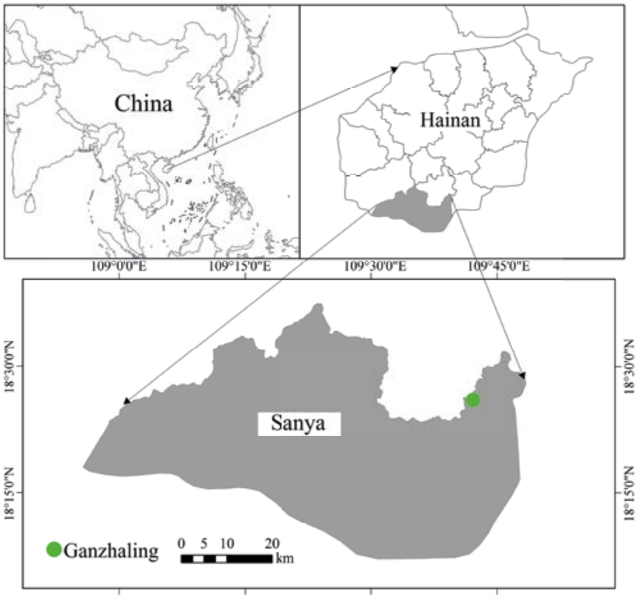


Figure 1: The study area location.

Abbildung 1: Die Lage des Untersuchungsgebiets.

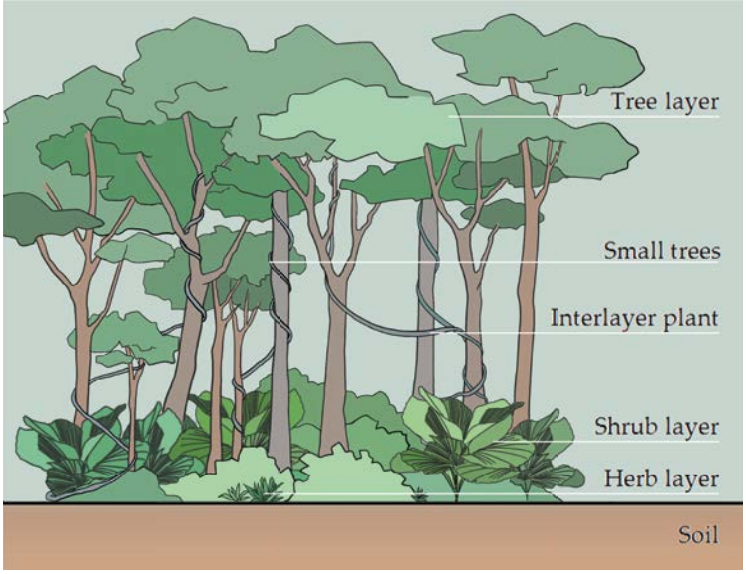


Figure 2: Schematic diagram of different stand layers considered in this study.

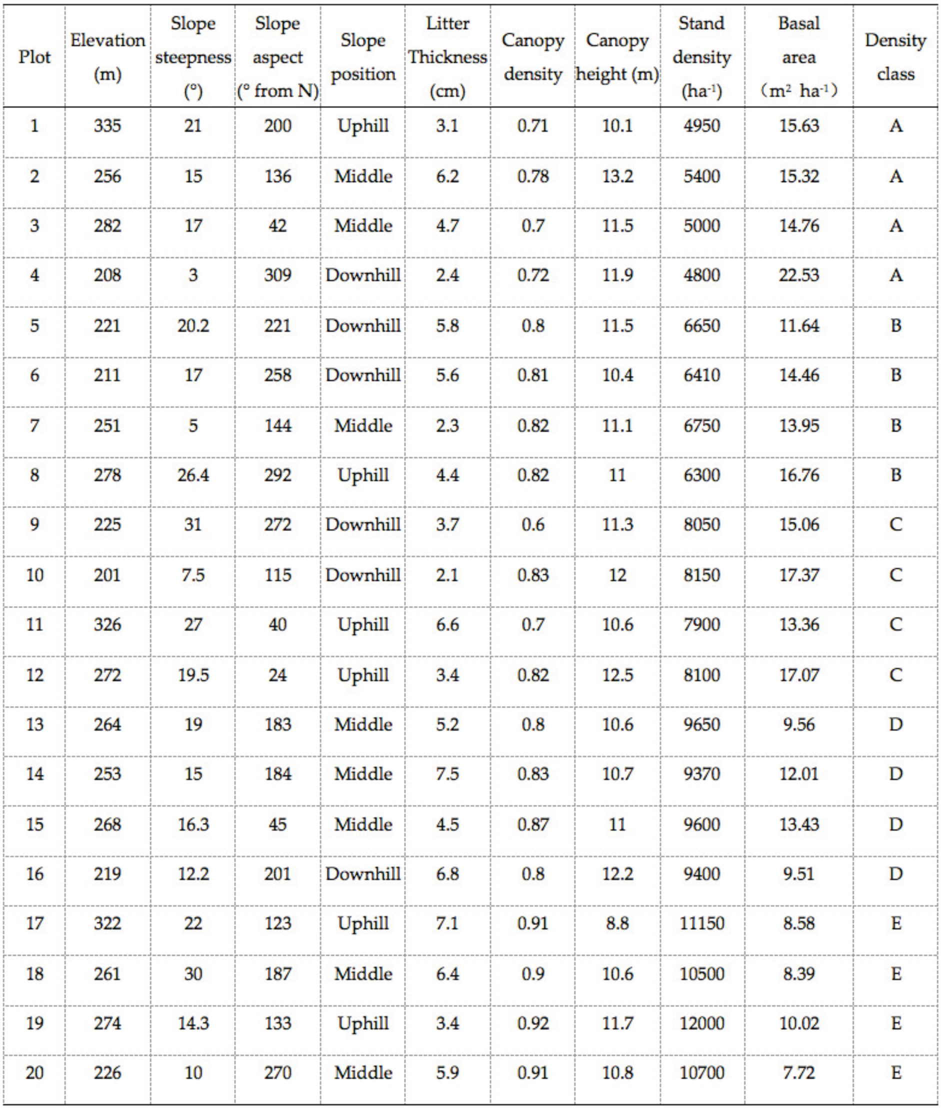
Abbildung 2: Übersicht der verschiedenen Bestandsschichten dieser Studie

2.2 Site selection

In April to June 2017, we selected four replicates of 20-m × 20-m stands of five densities (A, 5000 trees·ha^{-1}; B, 6500 trees·ha^{-1}; C, 8000 trees·ha^{-1}; D, 9500 trees·ha^{-1} and E, 11 000 trees·ha-1) (total plot number = 20). In each plot, we measured altitude, steepness, aspect, slope position, litter thickness and stand structure of the canopy (*Table 1*). The five stand densities (A to E) used in this experiment correspond to the average actual density of sampled plots 1–4, 5–8, 9–12, 13–16, and 17–20, respectively.

Table 1: Site and stand characteristics of the 20 investigated tropical rainforest stands (plots).

Tabelle 1: Standort- und Bestandseigenschaften der 20 untersuchten Plots in einem tropischen Regenwald.



Plot	Elevation (m)	Slope steepness (°)	Slope aspect (° from N)	Slope position	Litter Thickness (cm)	Canopy density	Canopy height (m)	Stand density (ha^{-1})	Basal area (m^2 ha^{-1})	Density class
1	335	21	200	Uphill	3.1	0.71	10.1	4950	15.63	A
2	256	15	136	Middle	6.2	0.78	13.2	5400	15.32	A
3	282	17	42	Middle	4.7	0.7	11.5	5000	14.76	A
4	208	3	309	Downhill	2.4	0.72	11.9	4800	22.53	A
5	221	20.2	221	Downhill	5.8	0.8	11.5	6650	11.64	B
6	211	17	258	Downhill	5.6	0.81	10.4	6410	14.46	B
7	251	5	144	Middle	2.3	0.82	11.1	6750	13.95	B
8	278	26.4	292	Uphill	4.4	0.82	11	6300	16.76	B
9	225	31	272	Downhill	3.7	0.6	11.3	8050	15.06	C
10	201	7.5	115	Downhill	2.1	0.83	12	8150	17.37	C
11	326	27	40	Uphill	6.6	0.7	10.6	7900	13.36	C
12	272	19.5	24	Uphill	3.4	0.82	12.5	8100	17.07	C
13	264	19	183	Middle	5.2	0.8	10.6	9650	9.56	D
14	253	15	184	Middle	7.5	0.83	10.7	9370	12.01	D
15	268	16.3	45	Middle	4.5	0.87	11	9600	13.43	D
16	219	12.2	201	Downhill	6.8	0.8	12.2	9400	9.51	D
17	322	22	123	Uphill	7.1	0.91	8.8	11150	8.58	E
18	261	30	187	Middle	6.4	0.9	10.6	10500	8.39	E
19	274	14.3	133	Uphill	3.4	0.92	11.7	12000	10.02	E
20	226	10	270	Middle	5.9	0.91	10.8	10700	7.72	E

2.3 Plant diversity

All trees of each plot with > 1 cm DBH (diameter at breast height at 1.3 m above ground) were sampled, with their individual DBH and species name recorded. Understory vegetation was assessed in three layers: shrubs, herbs, and interlayer plants. Herb species were recorded from five 2-m × 2-m quadrats located at the four corners and one in the center of each plot. Interlayer plants mainly included climbing vines and were measured at diameter 30 cm above ground.

We used α diversity as a measure of community species diversity of each plot, and species importance value (IV) to measure of local dominance, the latter calculated using the formulas reported by Ding and Song (1998) and Fang *et al*. (2009).

$$IV_{shrub} = (RD+RF+RB)/3$$

$$IV_{herb} = (RD+RF+RC)/3$$

where *RD* is the relative density, *RF* is the relative frequency, *RB* is the relative breast height diameter, and *RC* is the relative coverage. The *IV* value was used to calculate species diversity for each plot for shrubs and for herbs. We also calculated species richness (*S*), Shannon-Wiener (*H*), Simpson (*D*), and Pielou's equitability (*Jsw*) (Zhang, 2017).

S: expressed as relative species richness (number of species).

$$D = 1 - \sum_{i=1}^{s} P_i^2$$

$$H = -\sum_{i}^{S} p_i \log p_i$$

$$Jsw = \frac{-\sum p_i \log p_i}{\log s}$$

where $P_i = n_i/n$; i = 1, 2, 3, …

2.4 Soil sampling and analysis

The "S" sampling method was adopted to distribute the soil samples and a soil profile was dug at five points per plot was sampled in two layers from two depths (0–20 and 20–40 cm). By using a cutting ring with 5 cm diameter 100 cm^3 soil was collected from the center of each layer. The number of soil samples collected per plot was 10 (0-20 cm: 5 and 20-40 cm: 5), with in total of 200 soil samples were collected. We pooled 100 g of soil from each layer per plot into sealed plastic bags to form composite soil samples for analysis of pH, water content, organic matter (OM), total nitrogen (TN), total potassium (TK), available potassium (AK), total phosphorus (TP), and available phosphorus (AP) (State Forestry Bureau, 1999). All soil samples were treated with ball mill after air drying. Soil pH is measured with a pH meter with a water-soil ratio of 2.5:1. Soil water content is measured by the oven drying method. Soil organic matter is measured by K_2CrO_7-concentrated H_2SO_4 external heating method. Total nitrogen in the soil is digested with concentrated H_2SO_4 and measured by a continuous flow analyzer. Total phosphorus in the soil is boiled with concentrated H_2SO_4-$HClO_4$ and measured by a continuous flow analyzer. Total soil potassium was fused by sodium hydroxide and measured by flame photometric method. Available phosphorus in the soil is extracted with 0.5 mol/L $NaHCO_3$ and measured by a continuous flow analyzer. Soil available potassium was extracted with 1 mol/L NH_4OAc and determined by flame photometer.

2.5 Statistical analysis

Differences in species, and soil physical and chemical properties among the five stand densities were analyzed using one-way ANOVA and LSD (least significant difference) tests (significant at $P < 0.05$). Analyses were carried out in SPSS 11.01 and all presented data are means ± standard deviations.

Soil and environment factors were logarithmic transformed using decadal logarithm, hellinger conversion of understory species diversity index was performed by the decostand function from the 'vegan' package, and the residual analysis was completed by the rda function. The interpretation rate of the conversion factor in the rda calculation results was checked by envfit() function. Finally, ggplot2 and ggrepel packages were using for visualization with the R statistical software, version R3.6.1.

3. Results

3.1 Soil physical and chemical properties

A comparison for the surface soil (0-20 cm) showed no differences in soil pH, TN, TK, and AK among the stand densities. There were differences for the surface soil in water content, OM, TP, and AP (P-values < 0.05), where water content was largest at highest stand density (E: 11 000 trees·ha^{-1}), and the remaining variables were greatest in the moderately dense stand (C: 8000 trees·ha^{-1}) *(Table 2)*. There was no significant difference in physical and chemical properties between the bottom soil (20-40 cm) under different stand densities.

Table 2: Soil physical and chemical properties under different tropical rainforest stand densities. Different letters after the same indexes indicate significant differences between different stand densities in the same soil layer (P-values < 0.05).

Tabelle 2: Bodenphysikalische und bodenchemische Eigenschaften unter unterschiedlich dichten tropischen Regenwaldbeständen. Unterschiedliche Kleinbuchstaben zeigen signifikante Unterschiede zwischen den Bestandsdichten je Bodenschicht an (*P* < 0.05).

Density	Soil layer	Water content (%)	pH	Organic matter (g/kg)	Total nitrogen (g/kg)	Total phosphorous (g/kg)	Total potassium (g/kg)	Available phosphorous (mg/kg)	Available potassium (mg/kg)
A	0-20	77.51±12.03b	5.10±0.03a	9.73±0.71b	0.61±0.06a	0.06±0.02b	12.35±1.67a	2.74±0.19ab	76.82±5.35a
	20-40	171±8.89a	4.97±0.12a	8.77±0.39a	0.52±0.03a	0.05±0.01a	10.21±0.68a	1.13±0.07a	66.31±6.29a
B	0-20	91.94±7.06b	5.11±0.06a	10.04±1.47ab	0.82±0.06a	0.09±0.00ab	15.61±2.76a	3.73±0.55a	89.70±6.93a
	20-40	156±9.32a	5.22±0.14a	9.31±0.48a	0.69±0.04a	0.07±0.01a	13.46±0.76a	1.64±0.11a	92.14±7.64a
C	0-20	103.41±9.40ab	5.24±0.05a	12.21±1.56a	0.79±0.13a	0.11±0.00a	16.47±1.71a	3.95±0.54a	80.00±10.53a
	20-40	213±10.17a	5.16±0.09a	11.04±0.52a	0.71±0.05a	0.08±0.02a	14.75±1.05a	1.81±0.09a	85.02±9.93a
D	0-20	107.47±12.45ab	5.17±0.02a	11.49±1.10ab	0.66±0.05a	0.10±0.02a	13.40±1.66a	2.94±0.30ab	78.88±5.73a
	20-40	189±8.21a	5.09±0.17a	9.89±0.59a	0.53±0.04a	0.07±0.01a	12.28±1.12a	1.33±0.12a	73.57±5.37a
E	0-20	116.83±8.84a	5.07±0.06a	9.21±0.85b	0.59±0.07a	0.06±0.00b	12.34±1.94a	2.09±0.24b	70.85±4.50a
	20-40	218±10.41a	5.14±0.08a	8.92±0.38a	0.51±0.03a	0.06±0.01a	13.14±1.31a	0.92±0.08a	79.85±4.26a

3.2 Species composition

We recorded in total 179 species from 135 genera and 87 families with 55 species in the shrub layer, 22 species in the herb layer, and 46 species of interlayer plants. Shrub, herb, and interlayer plant species richness was greatest in the moderately dense stand (C: 8000 plants·ha^{-1}), and lowest at the highest tree density (E: 11000 plants·ha^{-1}), and we found that interlayer plant species richness was consistently greater than for herbs, especially with increasing stand density *(Fig. 3)*.

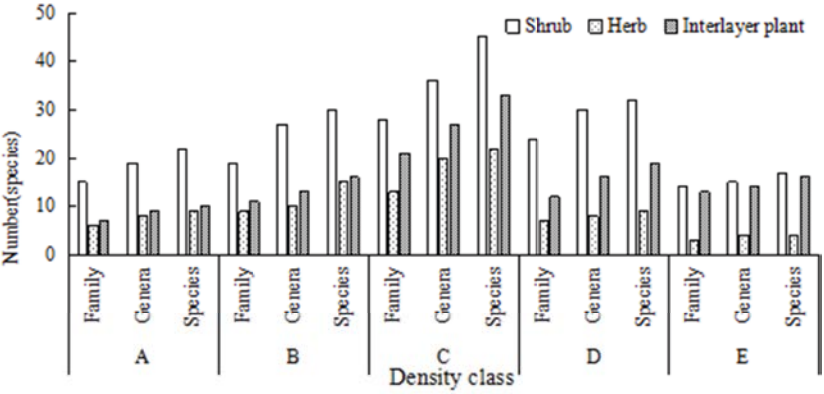


Figure 3: The number of families, genera and species in the understory vegetation under different stand densities in a tropical rainforest.

Abbildung 3: Die Anzahl Familien, Gattungen und Arten in der Unterschicht unter verschiedenen Bestandsdichten in einem tropischen Regenwald.

3.3 Species diversity

There were no differences in effect of stand density on either Shannon-Wiener or the Pielou's equitability indexes for the shrub layer, but there were differences in richness and the Simpson dominance indexes that were greatest in the moderately dense stand (C: 8000 trees·ha^{-1}). There were no differences in stand density effects on the Simpson dominance and Pielou's equitability indexes for the herb layer, but the richness and the Shannon-Wiener indexes were greatest at the moderately dense stand (C: 8000 trees·ha^{-1}). There was no effect of tree density on climber uniformity index, but there were differences in the richness and Shannon-Wiener indexes that were greatest at the higher stand density D (9500 trees·ha^{-1}), and on the Simpson dominance index that was greatest at the highest density (E: 11000 trees·ha^{-1}) *(Fig. 4)*.

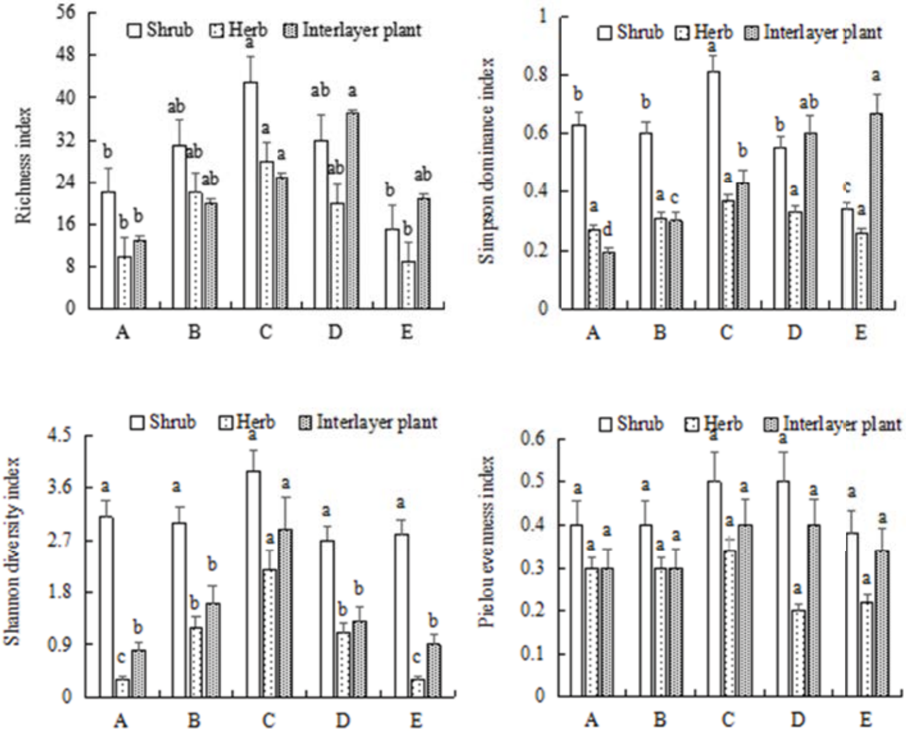


Figure 4: Effects of stand density on selected diversity indexes in a tropical rainforest. Different letters indicate differences at P < 0.05.

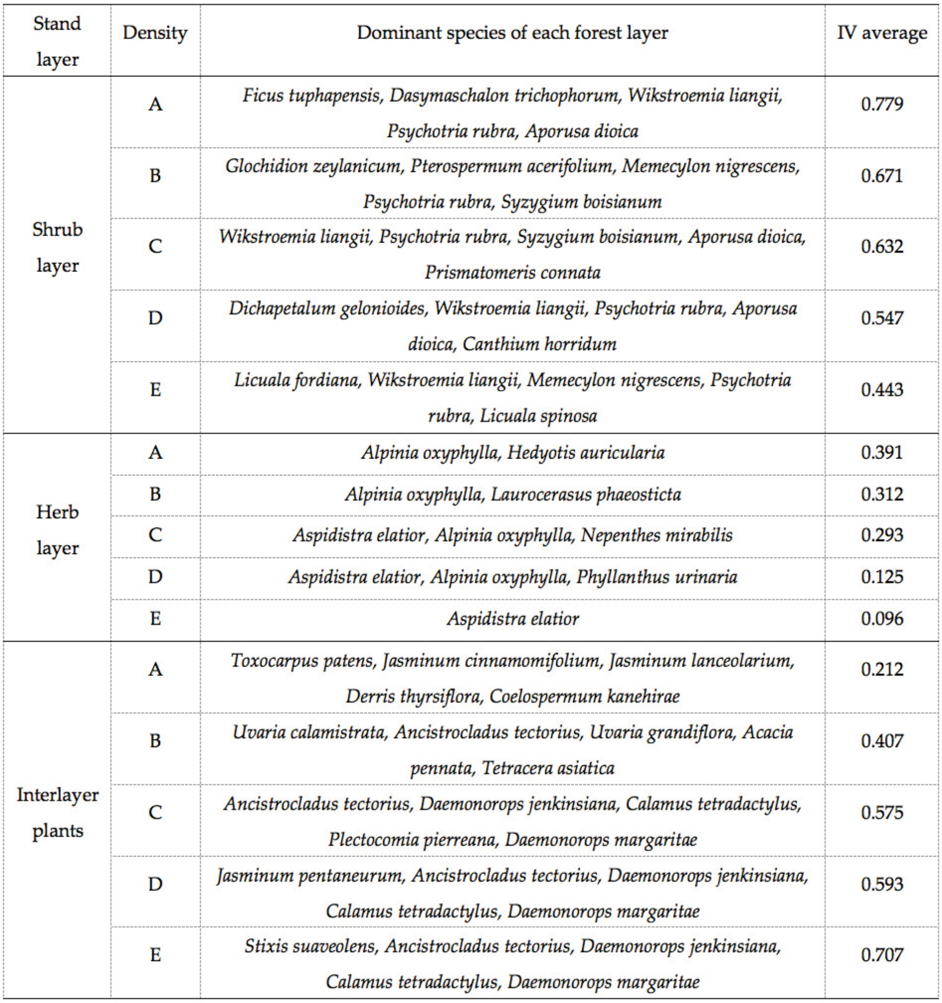
Abbildung 4: Auswirkungen der Bestandsdichte auf Artenvielfaltindizes eines tropischen Regenwaldes. Unterschiedliche Buchstaben zeigen signifikante Unterschiede ($P < 0.05$).

3.4 Species importance

Species' importance value (IV) varied with stand density and we found that the shrub layer was dominated by *Wikstroemia liangii*, *Psychotria rubra*, *Syzygium boisianum*, *Aporusa dioica*, and *Prismatomeris connate*; the herb layer was dominated by *Aspidistra elatior* and *Alpinia oxyphylla*; and interlayer plants were dominated by *Jasminum pentaneurum*, *Ancistrocladus tectorius*, *Daemonorops jenkinsiana*, *Calamus tetradactylus*, and *Daemonorops margaritae* (*Table 3*).

Table 3: Effect of stand density on importance value (IV) of understory vegetation in a tropical rainforest.

Tabelle 3: Einfluss der Bestandsdichte auf den Wichtigkeitswert (IV) in der Bodenvegetation in einem tropischen Regenwald.



Stand layer	Density	Dominant species of each forest layer	IV average
Shrub layer	A	*Ficus tuphapensis, Dasymaschalon trichophorum, Wikstroemia liangii, Psychotria rubra, Aporusa dioica*	0.779
	B	*Glochidion zeylanicum, Pterospermum acerifolium, Memecylon nigrescens, Psychotria rubra, Syzygium boisianum*	0.671
	C	*Wikstroemia liangii, Psychotria rubra, Syzygium boisianum, Aporusa dioica, Prismatomeris connata*	0.632
	D	*Dichapetalum gelonioides, Wikstroemia liangii, Psychotria rubra, Aporusa dioica, Canthium horridum*	0.547
	E	*Licuala fordiana, Wikstroemia liangii, Memecylon nigrescens, Psychotria rubra, Licuala spinosa*	0.443
Herb layer	A	*Alpinia oxyphylla, Hedyotis auricularia*	0.391
	B	*Alpinia oxyphylla, Laurocerasus phaeosticta*	0.312
	C	*Aspidistra elatior, Alpinia oxyphylla, Nepenthes mirabilis*	0.293
	D	*Aspidistra elatior, Alpinia oxyphylla, Phyllanthus urinaria*	0.125
	E	*Aspidistra elatior*	0.096
Interlayer plants	A	*Toxocarpus patens, Jasminum cinnamomifolium, Jasminum lanceolarium, Derris thyrsiflora, Coelospermum kanehirae*	0.212
	B	*Uvaria calamistrata, Ancistrocladus tectorius, Uvaria grandiflora, Acacia pennata, Tetracera asiatica*	0.407
	C	*Ancistrocladus tectorius, Daemonorops jenkinsiana, Calamus tetradactylus, Plectocomia pierreana, Daemonorops margaritae*	0.575
	D	*Jasminum pentaneurum, Ancistrocladus tectorius, Daemonorops jenkinsiana, Calamus tetradactylus, Daemonorops margaritae*	0.593
	E	*Stixis suaveolens, Ancistrocladus tectorius, Daemonorops jenkinsiana, Calamus tetradactylus, Daemonorops margaritae*	0.707

3.5 Redundancy analysis

We focused our analysis of the environmental factors on the surface soil (0-20 cm), as the difference of the bottom soil (20-40 cm) were not significant. In our redundancy analysis, the first and second spindles explained variance of 12.93% and 38.43% respectively (*Fig. 5*). SD (stand density) and CD (canopy density) were the main factor affecting the soil physical and chemical properties. SD, AP, TP and AK were negatively correlated, while WC, PH and TK were positively correlated. All analyzed soil nutrient metrics were correlated. CD was positively correlated with WC and negatively correlated with the soil physical and chemical properties. This may be due to the low light transmittance between gaps and transpiration rate in forests with high stand density, resulting in the increase of soil water content and the decrease of soil nutrient content. At the same time, we found that the LT (litter thickness) had a clear positive correlation with CD and SD and thus density seem to affect the decomposition and release of nutrients in the litter.

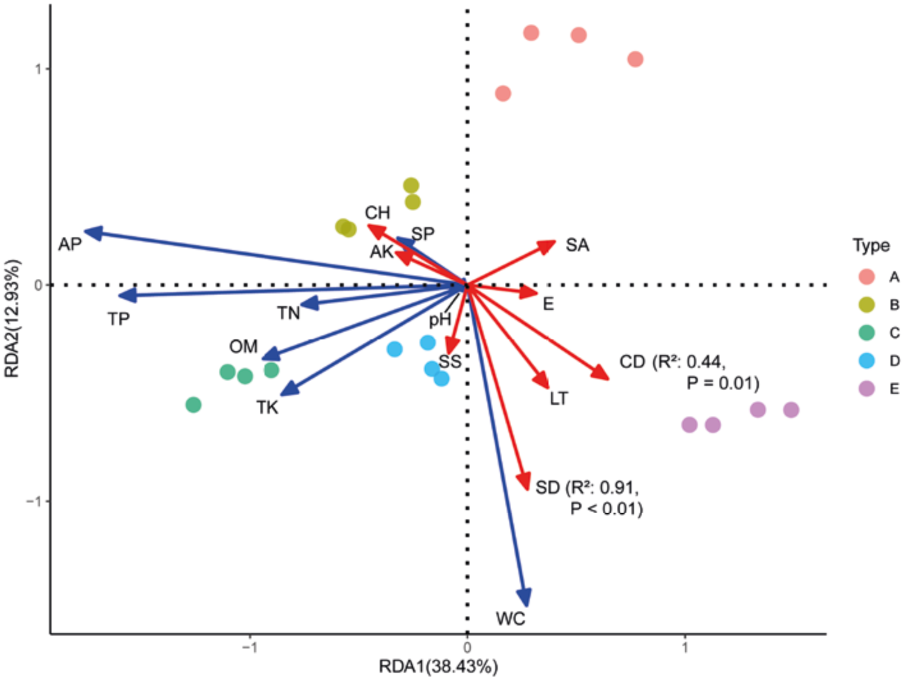


Figure 5: Redundancy analysis of environmental factors for the 20 sample plots. E is elevation, SS slope steepness, SA slope aspect, SP slope position, LT litter thickness, CD canopy density, CH canopy height, SD stand density, WC water content, OM organic matter, TN total nitrogen, TP total phosphorous, TK total potassium, AP available phosphorous, AK available potassium.

Abbildung 5: Redundanzanalyse der Umweltfaktoren für die 20 untersuchten Plots. E ist Seehöhe, SS Hangneigung, SA Hangrichtung, SP Handlage, LT Dicke der Streuschicht, CD Dichte der Oberschicht, CH Kronenhöhe, WC Wassergehalt des Boden, OM Organikanteil, TN Gesamtstickstoff, TP Gesamtphosphor, TP Gesamtkalium, AP Verfügbarer Phosphour, AK Verfügbares Kalium.

Focusing on the herb layer (*Fig. 6a*), the first and second spindles explained 38.79% and 19.45% of variance of the species diversity, respectively. Stand density (SD) and Simpson index (D) were positively correlated, and negatively correlated with Shannon-Wiener diversity (*H*), Pielou's equitability (Jsw) and species richness (*S*) and thus SD increases only one diversity index. SD inhibits *H* and *Jsw*. CD was also positively correlated with *D* and negatively correlated with *H*.

Focusing on the shrub layer (*Fig. 6b*), the first and second spindles explained 30.97% and 2.778% of variance of species diversity, respectively. SD and CD significantly affected species diversity, as SD was negatively correlated with *D* and *S*, and positively correlated with *H* and *Jsw*. Thus SD inhibited dominance (D) and richness (*S*) of shrub layer, while SD promoted diversity (*H*) and uniformity (*Jsw*) of shrub layer. Similar to SD, CD was positively correlated with *Jsw* and *H*, and negatively correlated with *S*.

Focusing on interlayer plants (*Fig. 6c*), the first and second spindles explained 70.06% and 7.886% of the variance variation of species diversity respectively. SD and CD significantly affected species diversity, as we noted a positive correlation between SD and *D*, and negative correlation between *H* and *Jsw*. SD promoted interlayer plant dominance (*D*), while SD inhibited interlayer plant diversity (*H*) and uniformity (*Jsw*). CD was positively correlated with *D* and *S*, and negatively correlated with *H* and *Jsw*.

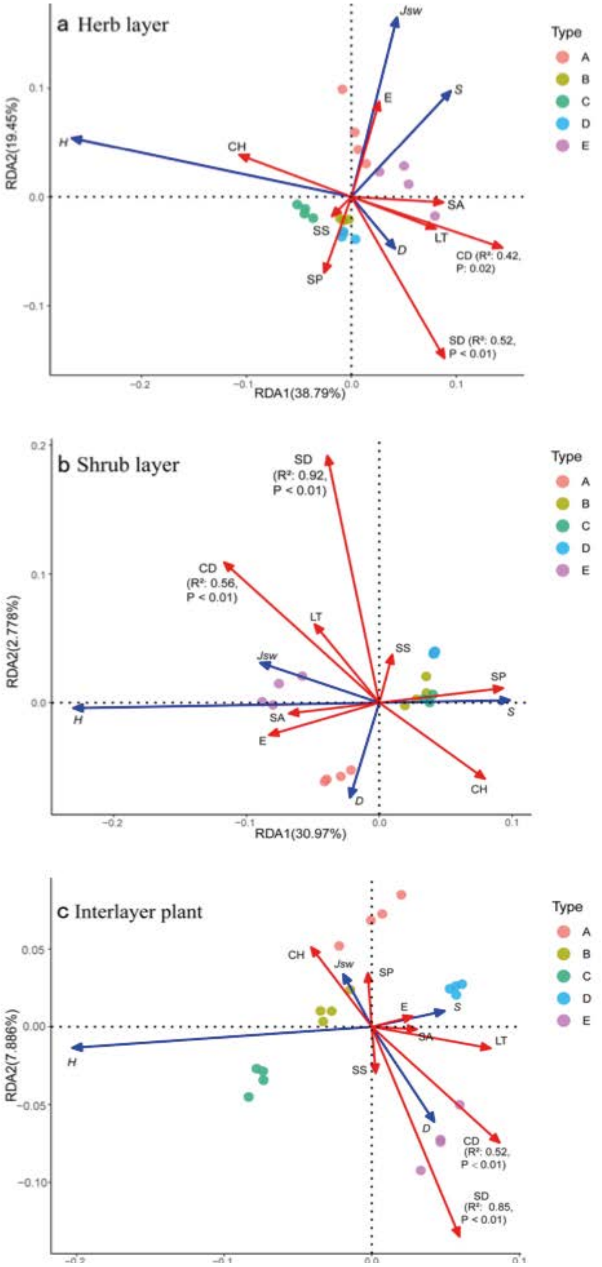


Figure 6: Redundancy analysis of understory species diversity and stand density.

Abbildung 6: Redundanzanalyse von Artenvielfalt in der Unterschicht und Bestandsdichte.

4. Discussion

4.1 Effects of stand density on soil physical and chemical properties in tropical rainforests

Stand density is a key driver of forest growth, because it affects airflow, light intensity, root growth, standing litter and decomposition rates and thus influence soil physical and chemical properties (Wei, 2012; Feng, 2018). Light transmittance and humidity under the canopy in turn affect the cycling of nutrients in the soil from litter decomposition (Andrew, 2015). Pristine, structurally diverse tropical rainforest stands have high temperature, humidity and stand density, where tree density drives forest characteristics and dynamics. The formation of habitats within forests leads to differences in soil spatial heterogeneity and physical and chemical properties (Sheng, 2001). In our study, we found that the soil water content increased with the increase of stand density, possibly as a result of a dense canopy and associated low levels of surface transpiration, while content of OM, TP, and AP was greatest at moderate stand density, supporting results of previous studies (Liu, 2010; Peng, 2017).

Forest litter is an important source of soil organic carbon pools and nutrients (Macinnis *et al.*, 2015). Litter decomposition is an important process determining litter accumulation in forest ecosystems and is affected by a range of environmental conditions and the chemical properties of the litter itself (Silver *et al.*, 2001; Sullivan *et al.*, 1999). The positive correlation between LT, SD and CD found in the study suggest that litter may be critical to explain the relationship between stand density and soil properties and litter measurements will be one of our future research directions.

4.2 Effects of stand density on tropical rainforest understory species diversity

Species diversity is an indicator of the complexity of community function and stability (Hao, 2014; Ou, 2014), and stand density is known to influence the growth and composition of understory vegetation by controlling light and moisture interception by trees (Zhou, 2017). With increasing canopy density, there were changes in the light intensity, humidity, soil nutrients and other conditions in the community, resulting in different understory microenvironments, species and distributions of shrub and herbs quantities (Wang, 2008). In our study, stand density affected herb species composition and abundance, both being greatest at the moderate level of stand density, while abundance was the lowest in the high density stand (11000 trees·ha^{-1}). These results indicate, that the effect of light on herb species survival is likely to be greater than other abiotic factors, such as water, and this drives understory species composition (Alem, 2015). We found that stand density had no effect on species diversity in the shrub layer; this may be beneficial to shrub layer growth in tropical high humidity and temperature environments. Our results that showed diversity of herb and climber species peaked at moderate levels of stand density are supported by previous studies of understory plant diversity indexes (Ding, 2018). By contrast, we found that the Simpson dominance index for climbing vine species increased with stand density, and peaked in the highest density plot, while the Shannon-Wiener diversity index for herbs and climbers in the low-density stand was low. These results indicate that tropical understory species do not thrive under extreme light conditions in the tropics (Kang, 2009). An appropriate forest density can improve the species diversity of a community, and therefore, optimizing forest structure is conducive to the succession of natural forest communities (Fang, 2009).

4.3 Relationships between stand environmental factors, understory species diversity and soil nutrients

Undergrowth vegetation is an important part of forest ecosystems and plays a key role in biodiversity, forest succession, nutrient cycling and maintaining site productivity (Gilliam, 2007). Stand density and canopy density were the main factors that affect understory species diversity and soil nutrients, but they had different effects on plant species diversity in three analyzed stand layers. Stand density promoted the dominance index of herbaceous layer and interlayer plants, but inhibited the diversity index and evenness index. Canopy density promoted the dominance index of herbaceous layer and interlayer plants, and inhibited the diversity index, but the situation of shrub layer was opposite. This may be because herbaceous plants cover the surface of the soil and have shallow roots, which can directly absorb nutrients from the surface of the soil, while shrub layers make use of nutrients from deeper layers (Yu, 2014).

The density of tropical rainforest stands varies and is the result of competition and resource utilization by various species in the forest community (Guo, 2007). The dominance of species change in different successional stages. For instance, when the density is low, ground vegetation, such as wild panax or interlayer plants can obtain more resources and become more dominant. The canopy layer development limits the extent of dominance in undergrowth species, until a new forest gap is created. Therefore, it is critical to understand the effects of stand structure and promote transition of community structure towards "potential natural vegetation" in the tropical rainforest, when protecting undergrowth species diversity is a management goal (Luo, 2013).

4.4 Effect of stand density on management of tropical lowland secondary rainforests

The sub-canopy forest environment is diverse, due to differences in species abundance and canopy density that result in the growth of multiple structural layers (Lu, 2007). In this study, species diversity, abundance and soil water content, organic matter, available phosphorus content were largest in the moderately dense stand (8000–9500 trees·ha^{-1}) and lowest at high and low stand density. The larger dominance of inter layer climbing plants in the high density stand may have restricted the growth of the canopy layer, since we recorded a relatively low (< 15 m) canopy height considering that about 40 years have passed since disturbance. This study suggests that 8000-9500 trees·ha^{-1} can be used as a reference for cultivating and improving quality of tropical lowland secondary rainforests. Currently most of the forests in this region of stand density greater 10,000 trees·ha^{-1}. Methods such as selective thinning and abandoning irrigation could be used to reach target stand density and improve the community structure of tropical natural forest towards the direction of the natural community.

5. Conclusion

Management of stand density may improve the understory environment, promote litter decomposition, and nutrient cycling, as we found that moderate stand density has positive effects on survival, growth, and regeneration of understory plants. Manipulating stand density may improve sub-canopy light penetration, humidity, and soil physical and chemical properties that benefit understory species abundance, diversity and stand stability and enhance the quality of secondary tropical rainforests. This study provide theoretical guidance and reference values for sustainable management of tropical lowland secondary rainforests.

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Branch development of eight-year-old *Mytilaria laosensis* plantations in response to planting density

Zweigentwicklung in achtjährigen *Mytilaria laosensis* Plantagen als Reaktion auf die Pflanzdichte

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Keywords: natural pruning, allometry, allocation patterns, branch characteristics, branch distribution, high-quality timber

Schlüsselbegriffe: natürliche Astreinigung, Allometrie, Allokationsmuster, Eigenschaften von Zweigen, Verteilung der Zweig, astfreies Holz

Abstract

Branch development is related to the formation of wood knots and affects timber quality and future market value of plantations and native forests alike. This study provides a theoretical basis and reference for knot-free timber production in a *Mytilaria laosensis* plantation. The branch diameter, length, angle, status (alive or dead), azimuth, and branch height under 12 m were measured for 60 dominant or co-dominant trees in response to five planting density treatments (625, 833, 1111, 1667, and 2500 stems ha^{-1}). With increasing planting density from 625 to 2500 stems ha^{-1}, the mean branch diameter and branch length decreased by 7.09% and 8.70% respectively. Dead and live branch angle decreased by 10.54% and 9.66% respectively, while number of living branches increased by 31.67% from 625 to 2500 stems ha^{-1}. Analyzing the spatial distribution using branch azimuth, we discovered that branches pointing north were more abundant and had larger diameter, larger branch length,

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and higher branch angle than branches pointing south. Branch diameter, length, and number were positively related to the relative branch height. Our results underline that increasing the planting density from 625 to 2500 stems ha^{-1} considerably affect branch growth. Thus, optimizing planting density when establishing *Mytilaria laosensis* plantations according to the forest management targets and future pruning can improve the timber quality and future value.

Zusammenfassung

Die Zweigentwicklung hängt mit der Bildung von Astlöchern und Knoten zusammen, die sich wiederum auf die Holzqualität und den zukünftigen Marktwert eines Bestandes auswirken. Ziel dieser Studie war es, eine theoretische Grundlage und Referenz für astfreie Holzproduktion einer *Mytilaria laosensis* Plantage zu erarbeiten. Wir untersuchten den Astdurchmesser, die Astlänge, der Astwinkel, den Status (lebendig oder tot) der Äste, die Orientierung der Äste sowie die Asthöhe unter 12 m für 60 dominante oder kodominante Bäume in fünf Pflanzdichtevariante (625, 833, 1111, 1667 und 2500 Stämme pro Hektar). Mit zunehmender Pflanzdichte von 625 auf 2500 Stämme ha^{-1} nahm der mittlere Astdurchmesser und die Astlänge ab (-7.09 % bzw. -8.70 %). Der Winkel wurde zunehmend spitzer sowohl für lebende als auch tote Äste (-10.54 % bzw. -9.66 %) und die Anzahl der lebenden Äste wurde um 31.67 % größer mit zunehmender Pflanzdichte. Hinsichtlich der räumlichen Verteilung der Äste zeigt sich, dass Äste in nördlicher Richtung höhere Astdurchmesser und Astlänge und geringere Astwinkel aufwiesen als Äste in südlicher Richrung. Durchmesser, Länge und Anzahl der Äste standen in positivem Zusammenhang mit der relativen Asthöhe. Diese Ergebnisse legen nahe, dass eine Erhöhung der Pflanzdichte von 625 auf 2500 Stämme ha^{-1} das Zweigwachstum deutlich beeinflusst. Die Wahl einer geeigneten Pflanzdichte beim Anlegen von *Mytilaria laosensis* Plantagen entsprechend den waldbaulichen Zielen und der Möglichkeit eines Astschnitt kann daher die Holzqualität und den Marktwert erhöhen.

Introduction

Mytilaria laosensis Lecomte is a fast-growing, broad-leaved tree species that has straight stem form and growing in China's South Subtropical Region (Guo *et al.* 2006). This species has been widely used for forestry transformation and timber production (Lin *et al.* 2000; Chen *et al.* 2012). High-quality and large-diameter *M. laosensis* timber is becoming increasingly popular on the markets. However, the low natural pruning capacity of *M. laosensis* results in the formation of many knots negatively affecting wood development and utilization.

Branches are a vital part of the canopy and support the leaves and reproductive structures. Tree vitality, growth, and stem form are determined by the distribution and size of the branches (Biging and Dobbertin 1992), which in turn affects tree growth and the forest stand volume (Wang *et al.* 2007). The quality and value of timber depend largely on the branches, as the diameter and number of branches along the stem are closely related to knot development (Hein 2008; Wang *et al.* 2016b). Dead branches, that are not shed, are gradually wrapped by the trunk cambium. Artificial pruning is a traditional forest management method critical for cultivating timber without knots, as it can reduce not only water and nutrient consumption (O'Hara 1991), but also the dead-knot defects of wood (Hein and Spiecker 2007). However, this method is time-consuming and costly. Therefore, studies of branch characteristics and distributions are critical to understand the growth characteristics and natural pruning. Stand density can control branch development and reduce costs for pruning and improve the quality of timber (Kellomäki *et al.* 1989).

Numerous factors influence branch development, including stand density (Mäkinen 1999a; Neilsen and Gerrand 1999; Alcorn *et al.* 2007), water and nutrient allocation to branches (Mäkinen *et al.* 2001), genotype (Alcorn *et al.* 2007; Gort *et al.* 2010), and other factors. For timber species, the lower part of stem below 6-8 m accounts for 90% of the future tree value (Kint *et al.* 2010). Thus, branch development in this region is essential for the early growth of trees and later utilization of the wood (Wang *et al.* 2018). Density control is an integral part of plantation management. Branch death and the speed of wound healing can be accelerated by high-density planting (Johansson 1992; Mäkinen 1999a). Although wide spacing is beneficial for the development of large-diameter wood, it can prolong branch death (Mäkinen 2002).

We previously investigated the effect of different planting densities on branch development in 'standard trees' of a six-year-old *M. laosensis* plantation (Wang *et al.* 2019). The definition of standard trees are trees with average diameter and tree height within the forest. Standard trees are representative for an unthinned forest. Selective target tree management and thinning has gained more attention from national and international forest researchers (e.g. De Freitas, 2004; David C, 2007; Liao SX, 2009). Dominant or co-dominant trees are the main crop trees for future harvesting, and suppressed trees may be removed by thinning. This approach can result in high-quality, large-diameter wood for the market, support sustainable forest management, and maximize the stability of forest ecosystems. We measured branch number, status (alive-dead), branch diameter, branch length, branch angle, azimuth, and height of first-order branches under 12 m of 60 dominant or co-dominant trees *M. laosensis* trees at different planting densities. We then tested the effect of five planting densities on branch development in this eight-year-old M. laosensis plantation. The results of the present study can provide an appropriate planting density for producing high-quality *M. laosensis* timber and reduce costs for artificial pruning.

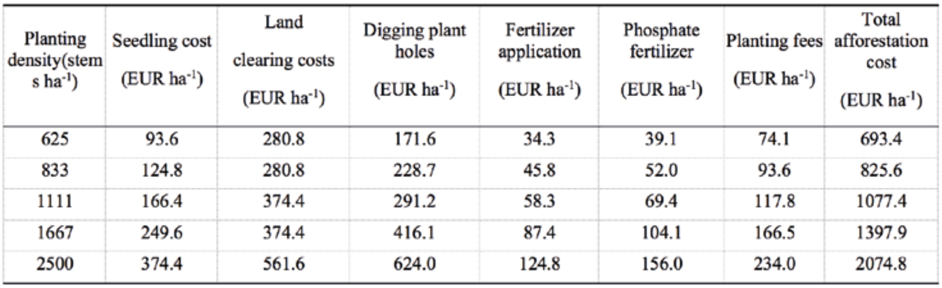
Materials and Methods

Experimental Site

The spacing trial was located at the SanKeng experimental base, XiJiang Forest Farm, Yunfu City, Guangdong Province, China (23°07′N, 111°51′E, Figure 1). The site is approximately 150–270 m above sea level and lies on a north slope with lateritic soil (pH 4.0). The study area has a south subtropical monsoon climate with an average annual temperature of 21.2°C and mean annual rainfall of 1600 mm. The mean annual air humidity is approximately 82%. Five planting densities (2500 ha^{-1} [2 × 2 m spacing], 1667 ha^{-1} [2 × 3 m], 1111 ha^{-1} [3 × 3 m], 833 ha^{-1} [3 × 4 m], 625 ha^{-1} [4 × 4 m]) were arranged in a randomized complete block design with four replicates in August 2010. The afforestation costs for five planting densities are shown in Table 1. Each plot was about 0.05 hectare. All trees in the experimental site were from the same provenance. One or two rows of trees of *M. laosensis* were planted around each plot for protection, so subject trees at plot edges were not influenced by neighboring plot circumstances.

Table 1: Plantation costs for five planting density treatments.

Tabelle 1: Plantagenkosten für fünf Pflanzdichtevarianten.



Planting density(stems ha^{-1})	Seedling cost ($EUR\ ha^{-1}$)	Land clearing costs ($EUR\ ha^{-1}$)	Digging plant holes ($EUR\ ha^{-1}$)	Fertilizer application ($EUR\ ha^{-1}$)	Phosphate fertilizer ($EUR\ ha^{-1}$)	Planting fees ($EUR\ ha^{-1}$)	Total afforestation cost ($EUR\ ha^{-1}$)
625	93.6	280.8	171.6	34.3	39.1	74.1	693.4
833	124.8	280.8	228.7	45.8	52.0	93.6	825.6
1111	166.4	374.4	291.2	58.3	69.4	117.8	1077.4
1667	249.6	374.4	416.1	87.4	104.1	166.5	1397.9
2500	374.4	561.6	624.0	124.8	156.0	234.0	2074.8

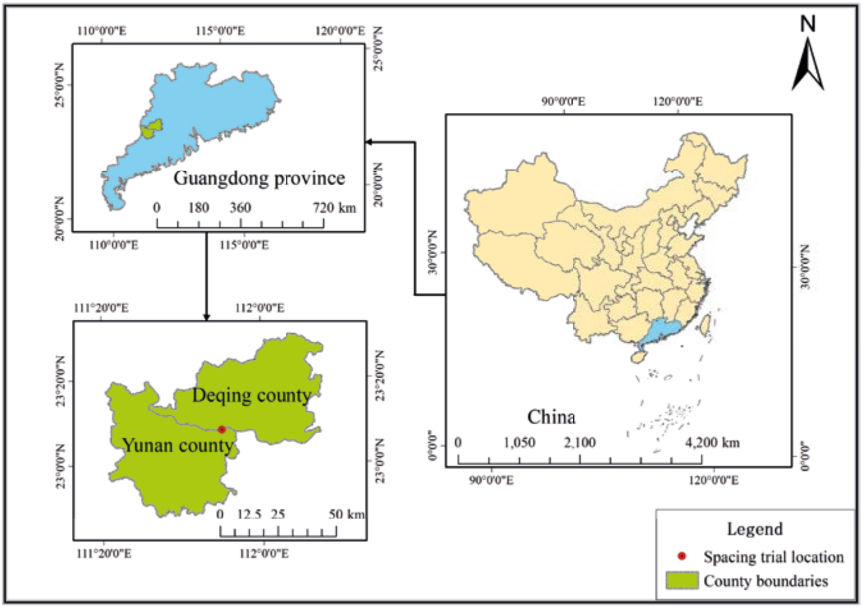


Figure 1: Location of M. laosensis spacing trial in Yunan County, Guangdong Province.

Abbildung 1: Die Lage des *M. laosensis* Pflanzdichteversuchs im Bezirk Yunan der Provinz Guangdong.

Measurements

Between July 13 and September 17, 2018 we measured diameter at breast height, tree height, height of the first live branch, and height of the first dead branch. Branch quantity (number, proportion), morphology (diameter, length, and angle), position (height and azimuth), and status (dead or alive) under 12 m of tree height were investigated in 60 dominant or co-dominant trees at five planting densities. Four plots were established for each of the five planting densities (in total 20 plots). Three dominant or co-dominant trees per plot were sampled for branch measurement. All sample trees were surrounded by healthy neighboring trees in all directions and only had a single leader; the trees were disease-free and had no broken tops. For each branch along the stem of the sample trees, the following variables were measured: branch diameter (30 mm from the base of each branch), branch length (length of primary branches), branch angle (from the branch base to the stem; a value of 0° indicates a perpendicular branch), relative branch height, and branch azimuth (0–360°). The azimuth was divided into eight intervals (0–45°, 46–90°, 91–135°,136–180°, 181–225°, 226–270°, 271–315°, and 316–360°). The status of each branch (dead or alive) was recorded and the numbers of live and dead branches were counted from the ground to the top of the sample tree. Live branches were defined as branches with green leaves;

dead branches were defined as branches with no green leaves.

Researchers used an extendable ladder to measure all branches on each tree in situ. The branch height and branch length were measured with a steel tape after using chalk to mark the stem at every 1 m, branch diameter was measured with an electronic Vernier caliper, and branch angle was measured with an electronic protractor. In total, 4363 branches (3312 dead branches and 1051 live branches) were measured from 60 dominant or co-dominant trees (3 trees per plot × 4 plots per treatment × 5 treatments).

Data Analysis

One-way analysis of variance (ANOVA) and Duncan's multiple range tests were performed to explore the differences in branch diameter, branch length, branch angle, number of live branches, and number of dead branches on stems below 12 m height among the five planting density treatments. The height of 12 m was used as the timber portion between the base of the stem up to a height of 6–8 m constitutes 90% of the future trees of commercial value (Kint *et al.* 2010). We used SPSS 20.0 (SPSS, Inc., Chicago, IL, USA) to determine the differences in height of first live branch, height of first dead branch, number of dead branches, number of live branches, number of total branches, and share of dead branches (ratio of dead branch quantity to total branches) among different treatments. We then analysed differences in branch diameter, branch length, branch angle, and branch numbers at different azimuth and heights by planting density.

Results

Tree growth and height of branches

Planting density significantly affected the stem diameter at breast height as well as height of first living branch for dominant or co-dominant trees in the *M. laosensis* plantation (Fig. 2). The stem diameter at breast height was negatively correlated with planting density from 22.0 to 18.0 cm, and stem diameter at breast height of 625 and 833 stems ha^{-1} treatment was significantly higher than those of other treatments ($P < 0.01$). The height of first living branch increased with the increasing planting density from 6.8 to 9.4 m. The treatment of 1667 stems ha^{-1} was not significantly (6.8%) higher than that of 2500 stems ha^{-1}($P > 0.05$). Thus, our results indicated that planting density did not significantly affect the height of first dead branch and tree height of dominant or co-dominant trees.

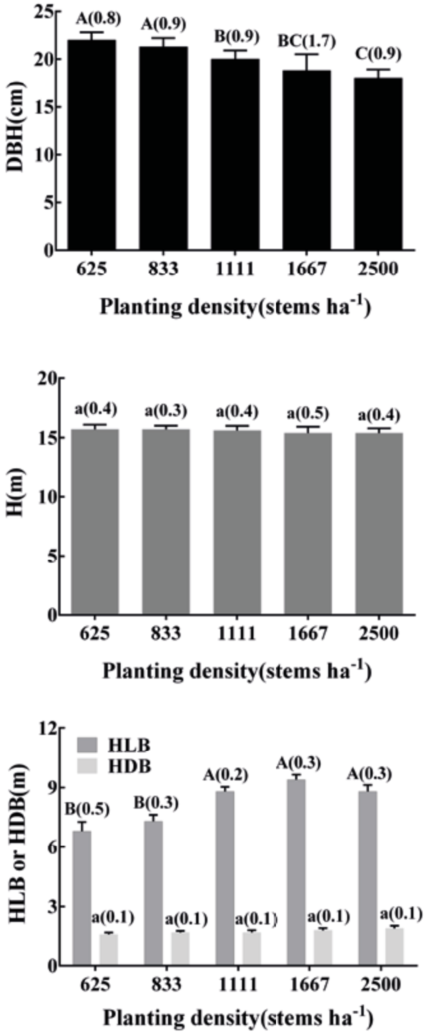


Figure 2: Diameter at breast height (DBH), tree height (H), height to first living branch (HLB) and height to dead branch (HDB) and associated analysis of variance of planting densities on dominant and co-dominant tree in a 8-year-old M. laosensis plantation. Standard error is shown in parentheses; different letters in the same column indicate significant differences between planting density treatments at the 0.01 level.

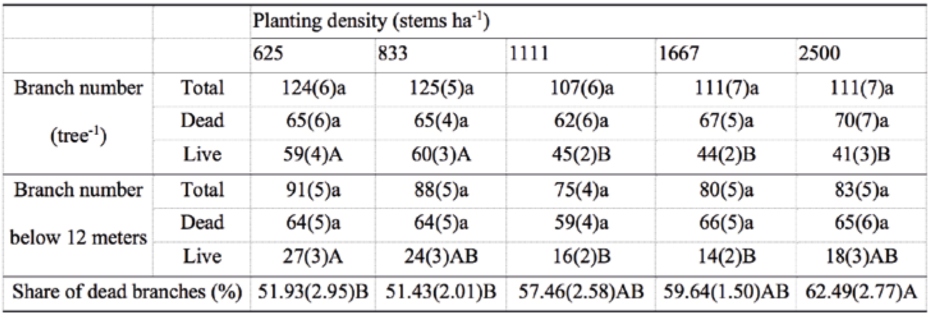
Abbildung 2: Brusthöhendurchmesser (DBH), Baumhöhe (H), Höhe des ersten lebenden Astes (HLB) und Höhe des ersten toten Astes (HDB) und deren Varianzanalyse bei unterschiedlichen Pflanzdichten von dominanten und kodominanten Bäumen einer 8-jährigen *M. laosensis* Plantage. Standardfehler in Klammer, unterschiedliche Buchstaben zeigen signifikante Unterschiede zwischen den Pflanzdichten bei 0.01 Signifikanzniveau.

Branch quantity

Planting density had no significant effect on the number of total branches, number of dead branches, and number of dead branches under 12 m among the five density treatments ($P > 0.05$). The number of live branches and number of live branches below 12 m were negatively correlated with planting density. The share of dead branches was positively correlated with increasing planting density. The highest density of dead branches was observed in the 2500 stems ha^{-1} treatment (Table 2), whereas there were no significant differences between the 1111, 1667, and 2500 stems ha^{-1} treatments.

Table 2: The main effect from analysis of variance of planting densities on branch number and share of dead branches of sample dominant or co-dominant trees of M. laosensis plantation. For details, we refer to table 1.

Tabelle 2: Der Haupteffekt der Varianzanalyse der Pflanzdichten auf die Anzahl der Äste und des Anteils abgestorbener Äste von dominanten und kodominanten Bäumen der *M. laosensis* Plantage. Für Details verweisen wir auf Tabelle 1.



		Planting density (stems ha^{-1})				
		625	833	1111	1667	2500
Branch number (tree^{-1})	Total	124(6)a	125(5)a	107(6)a	111(7)a	111(7)a
	Dead	65(6)a	65(4)a	62(6)a	67(5)a	70(7)a
	Live	59(4)A	60(3)A	45(2)B	44(2)B	41(3)B
Branch number below 12 meters	Total	91(5)a	88(5)a	75(4)a	80(5)a	83(5)a
	Dead	64(5)a	64(5)a	59(4)a	66(5)a	65(6)a
	Live	27(3)A	24(3)AB	16(2)B	14(2)B	18(3)AB
Share of dead branches (%)		51.93(2.95)B	51.43(2.01)B	57.46(2.58)AB	59.64(1.50)AB	62.49(2.77)A

Branch diameter, length, and angle

Planting density significantly affected the mean branch diameter and branch length of dead branches under 12 m of the stem for *M. laosensis* ($P < 0.01$). The mean branch diameter and branch length ranged from 17.95 to 19.32 mm and 1.47 to 1.61 m, respectively, and both showed a decrease with increased planting density. There were no significant differences in the mean dead branch diameter and branch length between 1667 and 2500 stems ha^{-1} treatments, and the branch diameter and branch length of the 1667 stems ha^{-1} treatment were only 2.1% and 1.4%, respectively, which were greater than those of the 2500 stems ha^{-1} treatment. However, the mean branch diameter and branch length of living branches were not significantly affected by planting density. In addition, there was a significant linear positive relationship between branch diameter and branch length (Fig. 3).

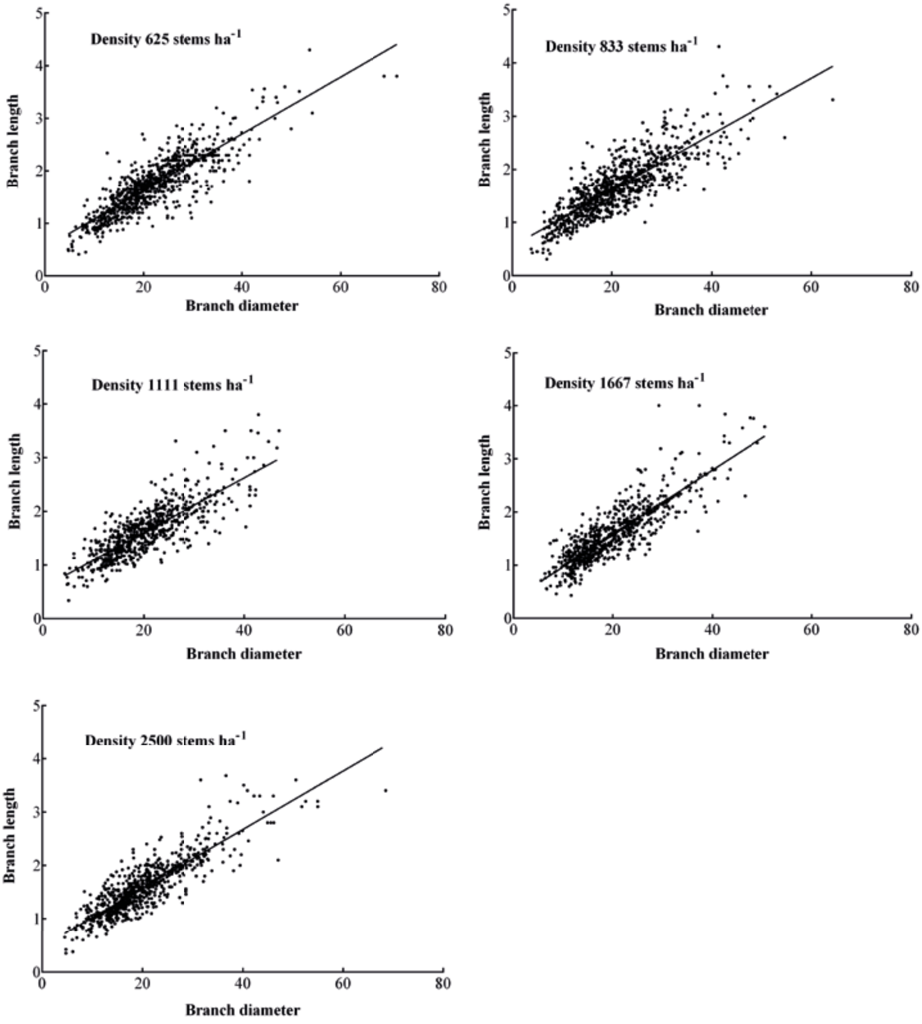


Figure 3: The positive correlation between branch diameter and branch length.

Abbildung 3: Die positive Korrelation zwischen Astdurchmesser und Astlänge.

The mean branch angles of both dead and living branches under 12 m were negatively correlated with planting density. The angles ranged from 50.85° to 56.84° and

45.91° to 50.82°, respectively. The branch angle at the lower density (625 and 833 stems ha^{-1}) was significantly larger than that in the other treatments, indicating that competition limits horizontal space available for branch growth with increasing planting density. The branch angle of living branches was more acute than that of dead branches at the same planting density (Fig. 4).

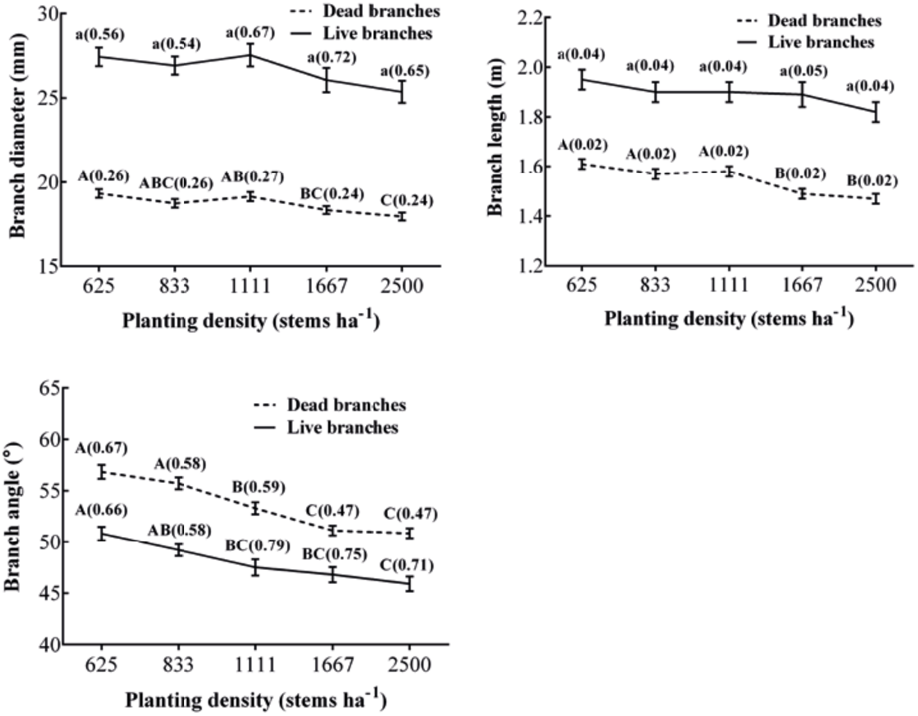


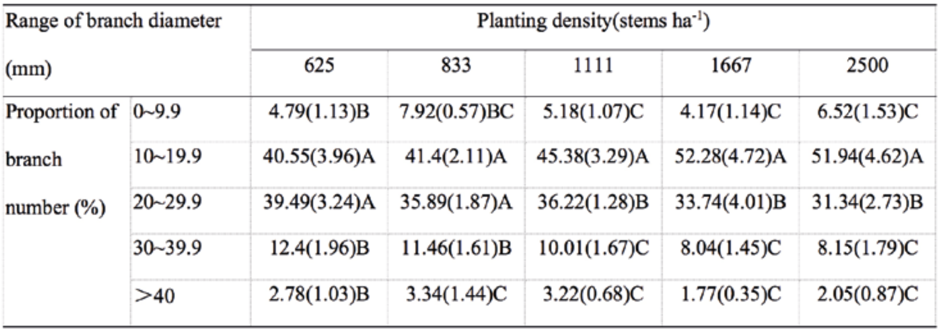
Figure 4: The main effect from analysis of variance of planting densities on branch diameter, length, and angle of dominant or co-dominant trees in the M. laosensis plantation. For details, we refer to table 1.

Abbildung 4: Der Haupteffekt aus der Varianzanalyse der Pflanzdichten auf Durchmesser, Länge und Winkel der Äste von dominanten oder kodominanten Bäume in der *M. laosensis* Plantage. Für Details verweisen wir auf Tabelle 1.

The proportions of branch number on the lower stem (≤12 m height) of the *M. laosensis* plantation first increased and then decreased with an increasing range of branch diameter at the same planting density. The branch number at the same planting density decreased in the order 10–19.9 > 20–29.9 > 30–39.9 > 0–9.9 mm. The proportion of branches with a branch diameter greater than 40 mm was lowest, showing a value of only 1–4% among the five planting density treatments. The proportion of branch number in the range of 10–19.9 mm was significantly different from that of 20–29.9 mm at medium and high densities (1111, 1667, and 2500 stems ha^{-1}, $P < 0.01$). We noted no significant difference at low densities (625 and 833 stems ha^{-1}), indicating that the frequency of the number of larger branches increased with decreasing planting density (Table 3). In contrast, the number of branches with diameters of 20–29.9 mm and 30–39.9 mm tended to decrease with increasing planting density. However, the number of branches with a diameter of 10–19.9 mm increased with increasing planting density and reached a maximum in the 1667 stems ha^{-1} planting density treatment.

Table 3: The main effect from analysis of variance of planting densities on proportion of branch number for different ranges of branch diameters of dominant or co-dominant trees in the M. laosensis plantation. For details, we refer to table 1.

Tabelle 3: Der Haupteffekt der Varianzanalyse der Pflanzdichte auf den Astanteil für verschiedene Astdurchmesserbereiche von dominanten oder kodominanten Bäume in der *M. laosensis* Plantage. Für Details verweisen wir auf Tabelle 1.



Range of branch diameter (mm)		Planting density(stems ha^{-1})				
		625	833	1111	1667	2500
Proportion of branch number (%)	0~9.9	4.79(1.13)B	7.92(0.57)BC	5.18(1.07)C	4.17(1.14)C	6.52(1.53)C
	10~19.9	40.55(3.96)A	41.4(2.11)A	45.38(3.29)A	52.28(4.72)A	51.94(4.62)A
	20~29.9	39.49(3.24)A	35.89(1.87)A	36.22(1.28)B	33.74(4.01)B	31.34(2.73)B
	30~39.9	12.4(1.96)B	11.46(1.61)B	10.01(1.67)C	8.04(1.45)C	8.15(1.79)C
	>40	2.78(1.03)B	3.34(1.44)C	3.22(0.68)C	1.77(0.35)C	2.05(0.87)C

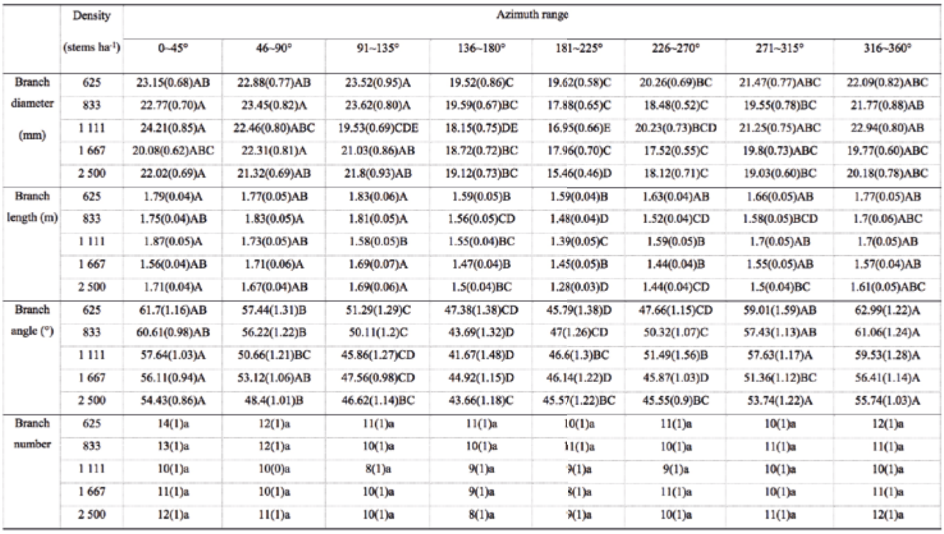
Branch Distribution

By analyzing the distribution of branch diameter, branch length, branch angle, and branch quantity with a different azimuth at the same planting density, we found that branches pointing towards the north had a larger diameter, longer branches, higher branch angle, and a higher number of branches than those pointing towards the south. The branch diameter and branch length of the five planting density treatments first decreased and then increased with an increasing azimuth angle. They reached a maximum value in the interval of 0–45° or 46–90° with good light conditions and decreased to a minimum value in the interval of 136–180° or 181–225°. Variance analysis showed no significant difference between the branch diameter and branch length in azimuth intervals 0–45°, 46–90°, 91–135°, and 316–360°. The branch angle reached a maximum value in the interval of 0–45° or 316–360° and decreased to a minimum value in the interval of 136–180°. The influence of different azimuth on branch number was not significant for the five planting density treatments (Table 4). Although branch number was not significantly affected by planting density, this value first decreased and then increased with increasing azimuth.

The branch diameter and branch length under the same planting density increased with increasing relative branch height, after which there was no significant change. The branch diameter reached a maximum at 8–10 or 10–12 m and decreased to a minimum at 0–2 or 2–4 m. The extreme difference in the vertical direction of branch diameter between the five planting density treatments was 5.68–7.31 mm. The branch length reached a maximum at 6–8, 8–10, or 10–12 m and decreased to a minimum at 0–2 or 2–4 m. The variation amplitude of branch length at each density in the vertical direction was 0.16–0.38 m. The branch angle and branch number for the same density treatment increased with increasing relative branch height (Table 5).

Table 4: The main effect from analysis of variance of different azimuth on branch characteristics for M. laosensis under the same planting density. For details, we refer to table 1.

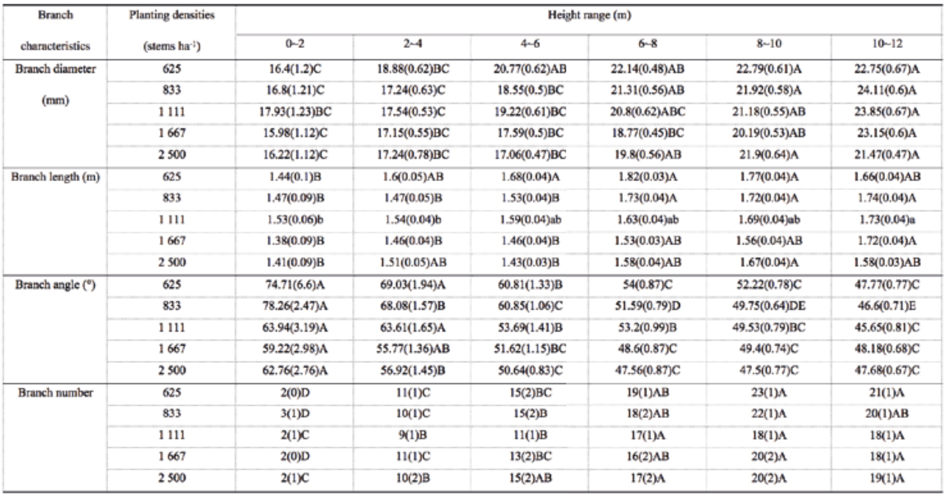
Tabelle 4: Der Haupteffekt aus der Varianzanalyse verschiedener Azimutwinkel auf die Asteigenschaften von *M. laosensis* unter der selben Pflanzdichte. Für Details verweisen wir auf Tabelle 1.



	Density	Azimuth range							
	(stems ha^{-1})	0~45°	46~90°	91~135°	136~180°	181~225°	226~270°	271~315°	316~360°
Branch diameter (mm)	625	23.15(0.68)AB	22.88(0.77)AB	23.52(0.95)A	19.52(0.86)C	19.62(0.58)C	20.26(0.69)BC	21.47(0.77)ABC	22.09(0.82)ABC
	833	22.77(0.70)A	23.45(0.82)A	23.62(0.80)A	19.59(0.67)BC	17.88(0.65)C	18.48(0.52)C	19.55(0.78)BC	21.77(0.88)AB
	1 111	24.21(0.85)A	22.46(0.80)ABC	19.53(0.69)CDE	18.15(0.75)DE	16.95(0.66)E	20.23(0.73)BCD	21.25(0.75)ABC	22.94(0.80)AB
	1 667	20.08(0.62)ABC	22.31(0.81)A	21.03(0.86)AB	18.72(0.72)BC	17.96(0.70)C	17.52(0.55)C	19.8(0.73)ABC	19.77(0.60)ABC
	2 500	22.02(0.69)A	21.32(0.69)AB	21.8(0.93)AB	19.12(0.73)BC	15.46(0.46)D	18.12(0.71)C	19.03(0.60)BC	20.18(0.78)ABC
Branch length (m)	625	1.79(0.04)A	1.77(0.05)AB	1.83(0.06)A	1.59(0.05)B	1.59(0.04)B	1.63(0.04)AB	1.66(0.05)AB	1.77(0.05)AB
	833	1.75(0.04)AB	1.83(0.05)A	1.81(0.05)A	1.56(0.05)CD	1.48(0.04)D	1.52(0.04)CD	1.58(0.05)BCD	1.7(0.06)ABC
	1 111	1.87(0.05)A	1.73(0.05)AB	1.58(0.05)B	1.55(0.04)BC	1.39(0.05)C	1.59(0.05)B	1.7(0.05)AB	1.7(0.05)AB
	1 667	1.56(0.04)AB	1.71(0.06)A	1.69(0.07)A	1.47(0.04)B	1.45(0.05)B	1.44(0.04)B	1.55(0.05)AB	1.57(0.04)AB
	2 500	1.71(0.04)A	1.67(0.04)AB	1.69(0.06)A	1.5(0.04)BC	1.28(0.03)D	1.44(0.04)CD	1.5(0.04)BC	1.61(0.05)ABC
Branch angle (°)	625	61.7(1.16)AB	57.44(1.31)B	51.29(1.29)C	47.38(1.38)CD	45.79(1.38)D	47.66(1.15)CD	59.01(1.59)AB	62.99(1.22)A
	833	60.61(0.98)AB	56.22(1.22)B	50.11(1.2)C	43.69(1.32)D	47(1.26)CD	50.32(1.07)C	57.43(1.13)AB	61.06(1.24)A
	1 111	57.64(1.03)A	50.66(1.21)BC	45.86(1.27)CD	41.67(1.48)D	46.6(1.3)BC	51.49(1.56)B	57.63(1.17)A	59.53(1.28)A
	1 667	56.11(0.94)A	53.12(1.06)AB	47.56(0.98)CD	44.92(1.15)D	46.14(1.22)D	45.87(1.03)D	51.36(1.12)BC	56.41(1.14)A
	2 500	54.43(0.86)A	48.4(1.01)B	46.62(1.14)BC	43.66(1.18)C	45.57(1.22)BC	45.55(0.9)BC	53.74(1.22)A	55.74(1.03)A
Branch number	625	14(1)a	12(1)a	11(1)a	11(1)a	10(1)a	11(1)a	10(1)a	12(1)a
	833	13(1)a	12(1)a	10(1)a	10(1)a	11(1)a	10(1)a	11(1)a	11(1)a
	1 111	10(1)a	10(0)a	8(1)a	9(1)a	9(1)a	9(1)a	10(1)a	10(1)a
	1 667	11(1)a	10(1)a	10(1)a	9(1)a	8(1)a	11(1)a	10(1)a	11(1)a
	2 500	12(1)a	11(1)a	10(1)a	8(1)a	9(1)a	10(1)a	11(1)a	12(1)a

Table 5: The main effect from analysis of variance of different height on branch characteristics for M. laosensis under the same planting density. For details, we refer to table 1.

Tabelle 5: Der Haupteffekt aus der Varianzanalyse unterschiedlicher Höhe auf Asteigenschaften für *M. laosensis* unter der gleichen Pflanzdichte. Für Details verweisen wir auf Tabelle 1.



Branch characteristics	Planting densities (stems ha^{-1})	Height range (m)					
		0–2	2–4	4–6	6–8	8–10	10–12
Branch diameter (mm)	625	16.4(1.2)C	18.88(0.62)BC	20.77(0.62)AB	22.14(0.48)AB	22.79(0.61)A	22.75(0.67)A
	833	16.8(1.21)C	17.24(0.63)C	18.55(0.5)BC	21.31(0.56)AB	21.92(0.58)A	24.11(0.6)A
	1 111	17.93(1.23)BC	17.54(0.53)C	19.22(0.61)BC	20.8(0.62)ABC	21.18(0.55)AB	23.85(0.67)A
	1 667	15.98(1.12)C	17.15(0.55)BC	17.59(0.5)BC	18.77(0.45)BC	20.19(0.53)AB	23.15(0.6)A
	2 500	16.22(1.12)C	17.24(0.78)BC	17.06(0.47)BC	19.8(0.56)AB	21.9(0.64)A	21.47(0.47)A
Branch length (m)	625	1.44(0.1)B	1.6(0.05)AB	1.68(0.04)A	1.82(0.03)A	1.77(0.04)A	1.66(0.04)AB
	833	1.47(0.09)B	1.47(0.05)B	1.53(0.04)B	1.73(0.04)A	1.72(0.04)A	1.74(0.04)A
	1 111	1.53(0.06)b	1.54(0.04)b	1.59(0.04)ab	1.63(0.04)ab	1.69(0.04)ab	1.73(0.04)a
	1 667	1.38(0.09)B	1.46(0.04)B	1.46(0.04)B	1.53(0.03)AB	1.56(0.04)AB	1.72(0.04)A
	2 500	1.41(0.09)B	1.51(0.05)AB	1.43(0.03)B	1.58(0.04)AB	1.67(0.04)A	1.58(0.03)AB
Branch angle (°)	625	74.71(6.6)A	69.03(1.94)A	60.81(1.33)B	54(0.87)C	52.22(0.78)C	47.77(0.77)C
	833	78.26(2.47)A	68.08(1.57)B	60.85(1.06)C	51.59(0.79)D	49.75(0.64)DE	46.6(0.71)E
	1 111	63.94(3.19)A	63.61(1.65)A	53.69(1.41)B	53.2(0.99)B	49.53(0.79)BC	45.65(0.81)C
	1 667	59.22(2.98)A	55.77(1.36)AB	51.62(1.15)BC	48.6(0.87)C	49.4(0.74)C	48.18(0.68)C
	2 500	62.76(2.76)A	56.92(1.45)B	50.64(0.83)C	47.56(0.87)C	47.5(0.77)C	47.68(0.67)C
Branch number	625	2(0)D	11(1)C	15(2)BC	19(1)AB	23(1)A	21(1)A
	833	3(1)D	10(1)C	15(2)B	18(2)AB	22(1)A	20(1)AB
	1 111	2(1)C	9(1)B	11(1)B	17(1)A	18(1)A	18(1)A
	1 667	2(0)D	11(1)C	13(2)BC	16(2)AB	20(2)A	18(1)A
	2 500	2(1)C	10(2)B	15(2)AB	17(2)A	20(2)A	19(1)A

Discussion

Height of first branch

Planting density had a significant effect on the stem diameter at breast height of the sampled dominant or co-dominant trees. Our results indicate that tree growth in the horizontal direction was inhibited by competition. Tree height was not significantly affected by planting density. This result is consistent with those of studies of planting or initial density and spacing for tree species such as *Eucalyptus pilularis* and *E. cloeziana* (Alcorn *et al.* 2007), *Betula alnoides* (Wang *et al.* 2018), six-year-old *M. laosensis* (Zhang *et al.* 2018), and young *Pseudotsuga menziesii* (Mirbel) Franco (Li *et al.* 2007). However, analysis of *Pinus taeda* L. by Antón-Fernández (2011) revealed differences between the dominant height and spacing, and these differences did not disappear with age. This may be because of the different characteristics of the tree species. Zhang (2018) found that dominant height was significantly affected in the first six years of *M. laosensis* growth.

There was no significant relation between planting densities and height of first dead branch, whereas height of first living branch was significantly increased with increasing planting density. This confirmed the results of Sun's study (2014) of *Cunninghamia lanceolata*, Mäkinen's study (1999b) of *Pinus sylvestris*, and Alcorn's study (2007) on *E. pilularis* and *E. cloeziana*, demonstrating that the mortality of branches on the lower stem increased with increasing stand density. However, the self-pruning ability of *M. laosensis* was lower than that of other tree species. Most dead branches on the lower stem were dry but not easily detached from the stem. Therefore, the capacity for self-pruning cannot be determined by the single indicator of the height of the first living branch but should also be comprehensively evaluated with multiple indicators, such as the height of the first dead branch and numbers of dead branches, living branches, and total branches.

Branch quantity

Branch quantity, particularly the number of dead branches hanging on the stem was closely related to wood quality. The number of total branches and number of dead branches in the 8-year old *M. laosensis* plantation did not differ significantly between the five planting density treatments. This result agreed with those of previous studies on planting density for some broad-leaf tree species such as 8-year old and 14-year-old *B. alnoides* (Wang *et al.* 2016b, 2018) and *Fagus sylvatica* (Kint *et al.* 2010). Our previous study of standard trees of an 8-year old *M. laosensis* plantation, Mäkinen and Hein's study (2006) of *Picea abies* (L.) Karst, and Hein's study (2008) of *Pseudotsuga menziesii* also showed that the branch number was mainly controlled by genes and a low correlation with environmental factors. Therefore, cultivating non-knot or lower-knot timber of *M. laosensis* by using density to control the branch number cannot be considered.

The number of live branches decreased significantly with increasing planting density. This result agreed with those of studies of *E. pilularis* and *E. cloeziana* (Alcorn *et al.* 2007), and *B. alnoides* (Wang *et al.* 2018), indicating that the forest environment affected the preservation of living branches. Light conditions at low density are better than those in higher density forests. Branches in the lower density groups have a wider growth space and longer survival time.

Branch characteristics

The branch diameter and branch length of dead branches were directly related to the formation of dead-knots. The branch diameter and branch length of dead branches of *M. laosensis* on the lower stem (≤12 m height) decreased with increasing planting densities, whereas those of living branches were not significantly affected by planting densities. This result is consistent with those of studies of 10-year-old *B. alnoides* (Wang *et al.* 2016a), 20-year-old *Pinus sylvestris* (Gort *et al.* 2010), young *Pseudotsuga menziesii* (Mirbel) Franco (Newton *et al.* 2012), and 4-year-old *Eucalyptus robusta* (Alcorn *et al.* 2007). Our previous study of standard trees of *M. laosensis* also showed that branch diameter and branch length were negatively correlated with planting density. However, the difference in branch diameter and branch length of standard trees at different planting densities was mainly reflected in the lower density (625, 833 stems ha^{-1}), medium density (1111, 1667 stems ha^{-1}), and higher density (2500 stems ha^{-1}), whereas the difference in dominant or co-dominant trees was reflected at lower density (625, 833 and 1111 stems ha^{-1}) and higher density (1667 and 2500 stems ha^{-1}). Because branch size was significantly positively correlated with the size of dead-knots in the timber, afforestation at high density may inhibit increases in branch diameter and reduce dead-knot wood problems in *M. laosensis*. Low density was conducive to cultivation of large-diameter timber, whereas higher density inhibited increases in branch size. The differences in branch diameter and branch length between the two higher planting density treatments (1667 and 2500 stems ha^{-1}) was not significant, whereas the afforestation cost of 1667 stems ha^{-1} density treatment was 32.62% lower than that at the 2500 stems ha^{-1} density.

The branch angle of both dead branches and living branches significantly increased with decreasing planting density. This may be because the reduction in planting density resulted in a larger space for growth and lowered the competition among branches in the horizontal direction. For *M. laosensis*, larger branches were heavier than smaller branches because of their larger number of leaves. Hence, the vertical pull of gravity may increase branch angle. Branch diameter was negatively related to planting density. Branches in the low-density forest were subjected to gravity in the vertical direction, which can also increase the angle between the branches and stem. In contrast, a larger branch angle made it easier for leaves to absorb sunlight. This result partly agrees with our study of standard trees of *M. laosensis* and Alcorn *et al.* (2007) and Henskens *et al.* (2001) studies of some eucalyptus species. However, Gort *et al.* (2010) evaluated *Pinus sylvestris* and found that branch angle was controlled by genes and not significantly affected by density. Wang *et al.* (2018) found in *B. alnoides* that although the branch angle was not significantly affected by planting density, lower planting density increased the branch angle.

Branch Distribution

In the horizontal direction, the branch diameter, branch length, and branch angle of *M. laosensis* on the side exposed to higher levels of sun at the same planting density and different azimuth were larger than those in the shade. The branch number was not significantly affected by the different azimuth range. Wang *et al.* (2018) evaluated 5-year-old *B. alnoides* and Xiao *et al.* (2006) evaluated *Pinus sylvestris* L. *var. mongolica* Litv. and found that the azimuth had no discernible effect on the number of primary branches. This result differs from our previous study of standard trees of an 6-year old *M. laosensis* plantation, in which the branch number of standard trees first decreased and then increased significantly in the horizontal direction with increasing azimuth. The dominant or co-dominant trees were taller than the rest, enabling the capture of more sunlight. For the large trees, the distribution of branches around the trunk was affected by the prevailing light conditions but not significantly. These branch indicators generally reached a maximum value in the azimuth angle of 0–45° but the maximum value of some densities were observed in the azimuth of 316–360° interval. This is because the slope of the test location is not an absolute north slope; there were subtle changes in the slope, which slowly changed the northeast slope into a northwest slope.

In the vertical direction, the branch number first increased gradually and then stabilized with increasing relative branch height. This result is consistent with that of Liu and Li (2007) for *Pinus sylvestris* L. *var. mongolica* Litv., where branches on the lower stems withered more than those in the crown. The branch diameter and branch length were significantly affected by the relative branch height. This finding partly agrees with those of studies of *Betula alnoides* (Wang *et al.* 2016b) and *E. pilularis* and *E. grandis* (Kearney *et al.* 2007), in which branch diameter and branch length increased significantly and branch angle decreased with increasing relative branch height. This also agrees with our previous study of standard trees of *M. laosensis*. For *Pseudotsuga menziesii* (Mirbel) Franco, Weiskittel *et al.* (2007) found that the branch angle was significantly negatively correlated with branch height.

Economic implications

Our results suggest that planting density should be determined according to the purpose of forest management or forest density should be adjusted by intermediate felling to control the branch size. Artificial pruning should be performed in young *M. laosensis* plantation when the branch diameter is low and the branches are rapidly growing. At this stage, the wound heals quickly and is less likely to be infected after pruning. Afforestation at a density of 1667 stems ha^{-1} can produce only approximately 2.1% larger branches than at 2500 stems ha^{-1}, but 32.62% of the cost could be saved on afforestation compared to that at 2500 stems ha^{-1}. Our findings provide a reference for density control, intensive management, and artificial pruning of *M. laosensis* plantations to enable production of high-quality and large-diameter timber. However, this was a static study of branch development in an 8-year-old *M. laosensis* plantation. As the fundamental aim of our study was to cultivate non-knot timber and improve timber quality, further studies of the relationship between phenotype features and knot formation are necessary. Additionally, the dynamic growth process of branch development with age should be evaluated.

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Conflicts of Interest

The authors declare that they have no conflicts of interest.

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Effects of different management treatments of post-fire soil respiration in a mixed forest ecosystem in northeastern China

Auswirkungen unterschiedlicher Bewirtschaftung auf die Bodenatmung nach einem Waldbrand in einem Mischwaldökosystem im Nordosten Chinas

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Keywords: *Larix gmelinii*, *Betula platyphylla*, permafrost, forest fire, salvage logging, soil temperature, soil moisture content, LI-COR, carbon sequestration

Schlüsselbegriffe: *Larix gmelinii*, *Betula platyphylla*, Permafrost, Waldbrand, Holznutzung, Bodentemperatur, Bodenfeuchte, Kohlenstoffsequestrierung

Abstract

Management of post-fire forest is essential for carbon cycling and forest ecosystem. Effects of post-fire logging on soil respiration have not been well studied, in particular in permafrost regions. We examined soil respiration rate, soil temperature and soil moisture during two growing seasons within the permafrost area of Daxing'anling in northeastern China. We were interested in the effects on soil respiration of (1) the forest fire and (2) the post-fire salvage logging. Soil respiration was measured by applying LI-8100 (LI-COR Inc.) measurement system. Heterotrophic soil respiration was measurement with the trenching method that cut off the roots resulting in root

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death without removing them. Our results indicated that the autotrophic soil respiration significantly increased after fire ($P < 0.05$). Selective-cutting increased both total soil respiration and heterotrophic soil respiration, while clear-cutting reduced soil respiration and both respiration components. Soil respiration of the selective-cut plot were significantly higher than that of the clear-cut plot ($P < 0.05$). Fire was associated with an increase in the share of autotrophic soil respiration, while salvage-logging of post-fire forest reduced this share, as the ratio of autotrophic soil respiration in the clear-cut plot was significantly lower than that in the unlogged area ($P < 0.05$). With increasing salvage logging intensity after fire disturbance, soil temperature increased. The varying and somewhat contradicting effects of different logging practices on soil respiration in burnt forest ecosystems require more studies to disentangle the effect of salvage logging and fire on soil respiration.

Zusammenfassung

Die Bewirtschaftung nach einem Waldrand ist wichtig für den Kohlenstoffkreislauf von Waldökosystemen. Die Auswirkungen von Holznutzung nach einem Feuer auf die Bodenatmung sind insbesonders für Permafrostregionen nicht gut untersucht. Wir haben die Bodenatmung, Bodentemperatur und Bodenfeuchtigkeit während zwei Vegetationsperioden im Permafrostgebiet von Daxing'anling im Nordosten Chinas gemessen, um die Auswirkungen von Waldbränden und Holznutzung nach einem Brand auf die Bodenatmung zu verstehen. Die Bodenatmung wurde mit einem LI-8100 (LI-COR Inc.) gemessen. Die heterotrophe Bodenatmung wurde mit der Grabenmethode gemessen, bei der durch Abtrennen die Wurzeln zum Absterben gebracht, aber nicht entfernt werden. Unsere Ergebnisse zeigten, dass die autotrophe Bodenatmung nach dem Waldbrand signifikant zunahm ($P < 0.05$). Die selektive Nutzung von verbrannten Bäumen erhöhte sowohl die gesamte Bodenatmung als auch die heterotrophe Bodenatmung, während Kahlschlag die Bodenatmung generell reduzierte. Die Bodenatmung auf selektiv genutzten Flächen war deutlich höher als jene von Kahlschlagflächen ($P < 0.05$). Waldbrand führte zu einem Anstieg des Anteils der autotrophen Bodenatmung, während die Nutzung nach dem Waldbrand die autotrophe Bodenatmung reduzierte und der Anteil der autotrophen Bodenatmung bei Kahlschlag deutlich niedriger als in nicht genutzten Beständen war ($P < 0.05$). Der Waldbrand führte zu einer Erhöhung der Bodentemperatur, die mit Intensität der Nutzung weiter anstieg. Die unterschiedlichen und teils widersprüchlichen Auswirkungen verschiedener Nutzungsformen auf die Bodenatmung in verbrannten Wälder erfordern weitere Studien zur Entflechtung der Auswirkungen von Waldbrand und Nutzung auf die Bodenatmung.

1. Introduction

Forests are the largest terrestrial ecosystem and slow down the pace of global warming by regulating global carbon balance and controlling the increase of atmospheric concentrations of greenhouse gases. Wildfire is a globally important disturbance in forest ecosystems. Many studies have shown that fire plays a crucial role in forest carbon fluxes (e.g. Kelly *et al*., 2016; Koster *et al*., 2018). The increasing surface temperature after fire disturbance has been reported to accelerate thawing of frozen soil in boreal forests, increase soil respiration, and ultimately lead to soil carbon loss (Aaltonen *et al*., 2019). After a forest fire, burnt trees remain dead standing in the forest and by occupying large areas continue to affect the soil carbon cycle. Accordingly, various post-fire management techniques (e.g., clear-cutting, selective-logging, afforestation) were used to restore the burnt forests, which inevitably affects soil respiration (Parro *et al*., 2019; Wittenberg *et al*., 2020). To recover economic losses and finance revegetation of the burned area, often post-fire managements involve 'salvage logging of the burned forest' (Garcia-Carmona *et al*., 2020; Martínez-García *et al*., 2017). However, such interventions in burnt forests have not been justified taking into account the effects on carbon dynamics and/or soil respiration.

Concilio *et al*. (2005) found that the soil respiration of mixed coniferous and broad-leaved forests increased after logging and burning, but the effect of burning was not significant. Salvage logging is a secondary disturbance to a post-fire forest, resulting in further reductions of tree biomass, a decrease in forest canopy density and an increase in surface radiation, which should affect the soil carbon cycle (Serrano-Ortiz *et al*., 2011; Stevens and Van, 2008). Lopez-Serrano *et al*. (2016) found that soil respiration increased after thinning on fire in mixed Mediterranean forests. Parro *et al*. (2019) reported soil respiration in burned and cleared areas was not reduced compared to burned and uncleared areas, while the soil respiration in unburned control areas was two times higher than that in burned areas. Therefore, both burning wood and cutting wood may have an effect on soil respiration in forest areas. Both forest fire and post-fire logging management could affect soil temperature, humidity, and nutrient content, which led to soil respiration volatility in forests and woodland (Hu *et al*., 2016; Lopez–Serrano *et al*., 2016).

The variability in soil respiration had been reported to be caused by changing soil temperature and soil respiration would raise exponentially with increasing soil temperature, given sufficient soil moisture (Hubbard *et al*., 2005). Eom *et al*. (2018) found that when the air temperature was high, the effect of precipitation on soil respiration was higher than that of soil temperature. Therefore, a regression model of soil respiration may provide a prediction of soil respiration dynamics, when considering the dominant factors such as temperature and moisture (Song *et al*., 2018). The combustion of organic matter and tree mortality caused by fire can lead to a decline in tree growth and reduction of soil autotrophic respiration (Tang *et al*., 2020). The release of soil CO_2 in forests after logging is affected by many factors, including regional climatic condition, local weather condition, soil carbon stock, groundwater level, tree age, species composition, local topography and logging intensity (Molchanov *et al*., 2017).

Clear-cutting may have a higher degree of interference with the accumulation of organic matter in mature trees than the fire disturbance, while the fire has greater effects on vegetation composition and soil structure (Haeussler and Bergeron, 2004). However, there are still controversies about the potential negative effects of post-fire logging management, regarding its impacts on vegetation restoration, soil properties and soil microbial characteristics (Francos *et al*., 2018). Lafleur *et al*. (2016) studied the effects of logging and fire disturbance on the northern forest and pointed out that fire is a 'chemical disturbance' while logging is a 'mechanical disturbance'. In the logging process, the forest floor is mechanically compacted. Furthermore, nutrients released by forest fires can be absorbed by the regenerating vegetation (Thiffault *et al*., 2007). The effects of salvage logging on soil respiration of burnt forest have not been well studied and the combined effect of fire and logging were not fully explored. In turn, the difference of the effects caused by the fire and logging, and the effect difference of different logging methods (clear-cutting, selective-cutting, or no-cutting) have not been clarified.

In this study, a burnt forest dominated by *Larix gmelinii* (distributed in Daxing'anling and Xiaoxing 'anling mountains, also found in Russia and far east China) on permafrost were selected as the study area. The research aims to (1) compare the temporal changes in soil respiration and its components at different salvage logging intensities, (2) investigate the effects of fire disturbance and salvage logging interference on soil respiration over 13 years and (3) analyze the association of soil respiration between soil temperature and moisture, respectively.

2. Material and Methods

2.1 Study Area

The study area located at the Kailaqi Forest Farm of the Genhe Forestry Bureau in Inner Mongolia, with the geographical position of east longitude:122°05′21″ ~ 122°04′46″, north latitude: 51°02′46″ ~ 51°01′08″ (Figure 1). The area is relatively flat, with elevations between 747 and 760 m. The area has a cold temperate and continental monsoon climate with an average annual temperature at -5.3 °C, the maximum daily temperature is 40 °C, and the minimum daily temperature is -58 °C. The average annual precipitation is 450 mm, which 12% as snowfall. The study area is located in a high latitude permafrost zone. Soil type is boralfs, which has a thin soil layer and a large number of gravel. Principal tree species are *Larix gmelinii* (*Larix gmelinii* (Rupr.) Kuzen.) and *Betula platyphylla* (Siberian silver birch) (Pan *et al*., 2013).

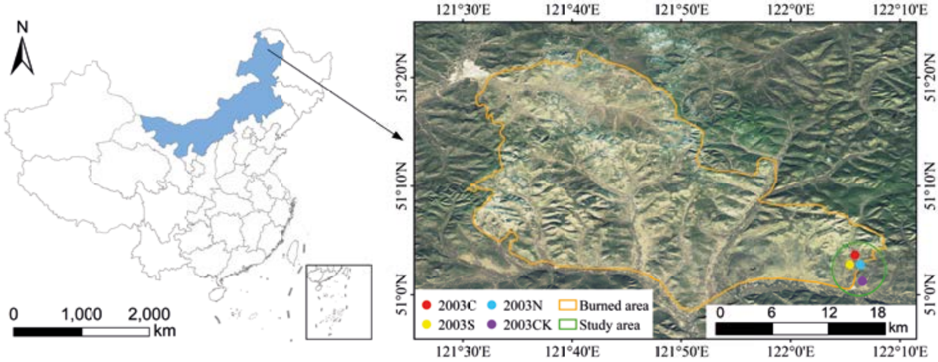


Figure 1: Location of study area und the burnt forest. The four experimental plots are located inside the green circle.

Abbildung 1: Lage des Untersuchungsgebiets und die Waldbrandfläche. Die vier Untersuchungsflächen liegen innerhalb des grünen Kreises.

2.2 Sample plots

The chosen wildfire site was the Jinhe-Genhe forest fire, that occurred in 2003. The wildfire happened on May 5, 2003, burning for seven days and covering an area of 1330 km² (east longitude: 121°29′24″ ~ 122°07′52″, north latitude: 51°22′12″ ~ 50°58′26″). Large-scale salvage logging management were conducted in the region in 2005, two years after the fire in 2003. There were three salvage logging methods implemented: clear-cutting, selective-cutting, and no-cutting. A control without burning and cutting was also established for comparison purpose. The three types of post-logging treatments were all light burned before cutting. Four sampling plots were set up in April 2016, ten years after the salvage logging occurred in 2005. The cutting intensity was 100% for the clear-cutting sample plot, 50% for the selective-cutting sample plot, 0% for the no-cutting sample plot and 0% for the control sample (unburnt-unlogged).

Three 30 m × 30 m observation sites were randomly distributed within each of the four treatments. The distance between the sample plots of the same treatment is about 10 m, the distance between the different treatments is about 500 m, giving a total of 12 observation sites (Figure 2, Table 1). An earlier field investigation in 2013 by Pan (2014) found that the 2003 forest fire affected soil respiration and that the soil respiration was still higher than the pre-fire level ten years after the fire. However, the effects of salvage logging (studied in the current study) were not measured in this earlier study.

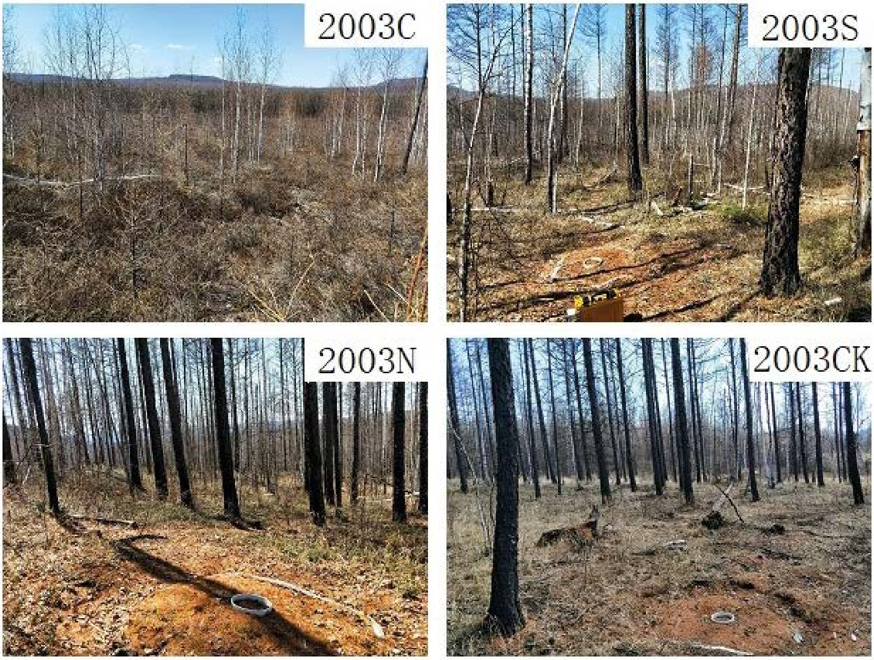


Figure 2: Field pictures of the four types of sample sites (photo taken in May 2018). 2003C is the clearcut, 2003S selective logged, 2003N unlogged and 2003CK the control site. At 2003C, small trees are not the original burnt wood, but newly re-generated trees. White rings show soil respiration measurement systems.

Abbildung 2: Photos der vier Probenstandorte (Foto vom Mai 2018). 2003C ist der Kahlschlag, 2003S wurde selektiv genutzt, 2003N nicht genutzt und 2003CK ist der Kontrollstandort. Bei2003C sind die kleine Bäume nach dem Brand gewachsen und nicht dieursprünglich verbrannten Bäume. Weiße Ringe zeigen Bodenatmungsmesssysteme an.

Table 1: Site characteristics of the four treatments (3 samplings sites per treatment).

Tabelle 1: Standorteigenschaften der vier Behandlungsvarianten (3 Probestellen pro Variante).

Sample type	Treatment	Altitude (m)	Slope gradient (°)	Aspect
2003C	Burnt, clear-cut	754	12	southwest slope
2003S	Burnt, selective-cut	752	13	southwest slope
2003N	Burnt, no-cut	760	13	southwest slope
2003CK	Unburnt, uncut control	747	8	southwest slope

An evaluation of species diversity found a total of 35 species of understory vegetation in the four experimental plots, belonging to 18 families and 32 genera. We measured factors (altitude, slope, slope direction) of each sample plot, and tree species and the number of regeneration trees (Table 2).

Table 2: The number of trees and undergrowth biomass of the 30 m×30 m sample plots. We show annual means with standard deviations. Letters (a, b, ab) show significant differences among salvage logging sample sites in the same line (Tukey's HSD test). P-values were considered significant at α = 0.05. For the methods used for vegetation biomass and litter, we refer to the appendix.

Tabelle 2: Die Stammzahl und die Biomasse der Bodenvegetation und Streuschicht auf den 30 m × 30 m großen Plots. Die Werte sind jährliche Mittelwerte mit Standardabweichungen. Die Buchstaben (a, b, ab) zeigen signifikante Unterschiede zwischen den Probenahmestellen für die Bergungsprotokollierung in derselben Zeile (Tukey-HSD-Test). P-Werte wurden bei α = 0.05 als signifikant angesehen. Für die Methoden der Bodenvegetation und Streuschicth verweisen wir auf den Appendix.

	Species	2003C	2003S	2003N	2003CK
Number of burned trees (live)or unburnt trees (trees/ha)	*Larix gmelinii*	0	700±300b	833±153b	1233±666a
	Betula platyphylla	0	389±77b	500±173a	337±55b
	Sum	0	1089±369b	1333±115a	1570±638bc
Number of regeneration trees (trees/ha)	*Larix gmelinii*	1100±176a	411±252b	411±241b	11±8c
	Betula platyphylla	400±67a	433±305a	400±200a	33±33b
	Sum	1500±133a	844±535b	811±430b	44±40c
Undergrowth shrub and grass biomass (t/ha)	Shrub	3.03±0.26a	2.09±0.78a	2.15±0.45a	0.32±0.34b
	Grass	0.27±0.06a	0.21±011a	0.26±0.04a	0.39±0.17a
	Sum	3.30±0.30a	2.30±0.83a	2.41±0.42a	0.71±0.51b
Litter (t/ha)	Total	16.24±2.51c	37.86±3.93b	35.82±7.88b	53.81±5.99a

2.3 Method of soil respiration measurement

Soil respiration was measured by applying LI-8100 (LI-COR Inc.) soil respiration measurement system (Astiani *et al*., 2015). At the end of April 2016, three groups of soil respiration ring were installed in each sample plot (three rings used to measure total soil respiration, and three rings to measure heterotrophic soil respiration, each ring had a diameter of 20 cm and height of 13.5 cm). Each ring was inserted vertically into the soil, leaving 2 cm of the ring above the ground for soil respiration observation. Sets of soil respiration rings were randomly arranged in the sample plot in the form of an isosceles triangle, with a 10 m spacing between individual rings.

The measurement of the heterotrophic respiration used the trenching method (Figure 3). We selected a 1 m diameter circular area within 2 m of each soil respiration ring. Then in the circular area, a 30 cm wide trench was dug with a shovel until 0.4 m-0.6 m depth, based on earlier investigation, that roots in this area are mainly distributed in the soil layer of 0-10 cm, and at 40 cm the soil parent material is reached. Then the roots in the trench were cut off, but not removed, and then a solid plastic film was placed in the trench to prevent any roots from growing into the 1m-diameter circular soil column (Kuzyakov, 2006). Above ground vegetation on the undisturbed soil column was removed, and regularly cleaned up, in order to remove any autotrophic respiration from herbaceous vegetation. The measurement period spanned the growing season (May – October), for two years (2016, 2017). To observe the effect of freezing-thawing on soil respiration, the month of April was added to the soil respiration observation in 2017. Measurements were taken 2-3 times per month, from 8:00 a.m. - 12:00 a.m. on each sampling day.

Autotrophic respiration rate (RA) was calculated as:

$$RA = RS - RH \qquad (1)$$

$$RA\% = (RS - RH)/RS \times 100\% \qquad (2)$$

Where RS represents total soil respiration rate (μmol $m^{-2}s^{-1}$), while RH is soil heterotrophic respiration rate. In equation (2) RA% represents the contribution ratio of soil autotrophic respiration relative to the total soil respiration (RS) (Han *et al*., 2018).

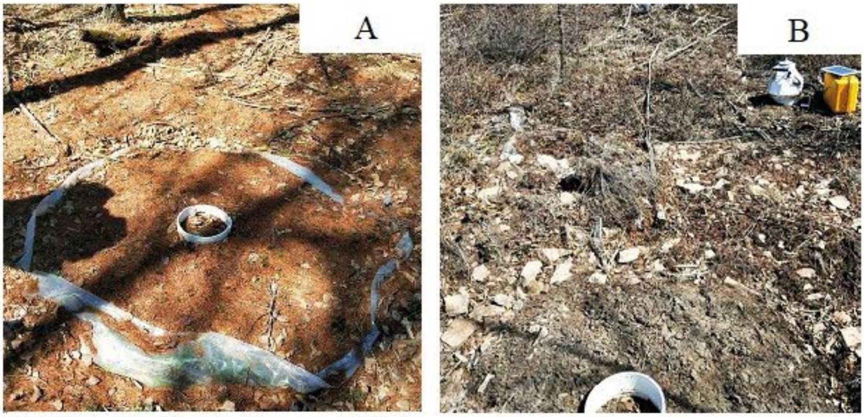


Figure 3: Pictures of soil rings for soil respiration measurements. A show the layout of heterotrophic soil respiration measurements using the trench method. B show a total soil respiration ring in the front.

Abbildung 3: Bilder der Bodenringe für Bodenatmungsmessungen. A zeigt einen Standort zur Messung der hetereotrophen Bodenatmung mit der Grabenmethode. B zeigt im Vordergrund einen Messring für die gesamte Bodenatmung.

2.4 Soil temperature and moisture observation

While observing soil respiration, we used a hand-held electron temperature probe (JM-222) to measure soil temperature at 10 cm depth (T_{10}) at each experiment plot. A time-domain reflectometry sensor (TDR300, Spectrum, Aurora, USA) was used to measure soil moisture at a depth of 10 cm near each soil respiration ring (W_{10}), and an averaged moisture value was obtained from all W_{10} measurements to represent each observation plot. The relationships between soil respiration rate (or its respiration components) and soil temperature or moisture were obtained based on the measured data; a regression model simulation of soil respiration was done as follows (Muñoz-Rojas *et al*., 2016).

$$R = \alpha e^{\beta T} \qquad (3)$$

$$Q_{10} = e^{10\beta} \qquad (4)$$

$$R = aW^2 + bW + c \qquad (5)$$

$$\ln(\mathrm{RS}) = \mathrm{d} + \mathrm{e} \times T + f \times W + h \times TW \qquad (6)$$

In equation (3) R is a random value of the RS, RA or RH rates, T represents the soil temperature (°C), α is the respiration rate at 0 °C, and β is a temperature response coefficient from which the temperature sensitivity coefficient Q10 can be obtained by equation (4), which indicates the sensitivity of soil respiration to temperature. The sensitivity index Q10 varies among different forest communities, different soil respiration components for the same community (Muñoz-Rojas *et al*., 2016). Equation (5) is a quadratic function of fitting R and soil moisture; a, b, and c are fitting constantly, and W is soil moisture (%). Equation (6) is a stepwise regression model, ln (RS) represents the natural logarithmic conversion of soil respiration rate, and d, e, f and h are fitting constantly (Wang *et al*., 2002).

3. Results

3.1 Dynamics of soil respiration and its components in the growing season

Monthly mean RS, RH and RA at different salvage logging sample plots and control sample plot showed a single peak in the 2016 growing season. However, the peak months of each soil respiratory component were different (Figure 4), the first rising appeared in May – July (for RS and RH) and then decreased in August – October, but the peak of the RA component appeared in September. In July, the RS and RH of 2003S plot were significantly higher than that of 2003N, 2003C and 2003CK plot. The RA of 2003N plot was significantly higher than that of 2003C and 2003CK plot ($P < 0.05$). During the growing season of 2017, RS and RH in all plots showed a two-peak pattern, the first peak appearing in May and the second in August. RS and RH in 2003S plot were significantly higher than that in 2003C sample plot in May and June. The two-year data showed that RS and RH were higher in July and August (Figure 4).

The average annual-mean (or season-mean) RS appeared to be the largest at the selective-cutting plot 2003S, followed in turn by no-cutting 2003N, control 2003CK, and clear-cutting 2003C, the RS of 2003S plot is significantly higher than that of 2003C plot (Table 3). Partly similar to RS, the average annual-mean RH was the largest one at 2003S, followed by 2003CK, 2003N and 2003C. Moreover, RH in 2003S plot was significantly higher than that in 2003C plot, but the annual-mean RA showed a different pattern: largest at 2003N followed by 2003S, 2003CK and2003C, RA in 2003N plot was significantly higher than that in 2003C plot. For all respiration components, the burnt clear-cut produced the lowest rates compared to the other three plots, while the burnt selective-cut produced the most considerable rate (except for the RA). Based on two years of observation data, there are significant differences between 2003S plot and 2003C plot for both RS and RH, 2003N plot and 2003C plot for RA (Table 3). The differences between the two observation years may due to the inter-annual climate differences (Figure 5). Average air temperature in 2017 (9.5 °C) was higher than that in 2016 (6.04 °C). Air relative humidity is 66.08% and 65.07% in 2016 and 2017 respectively.

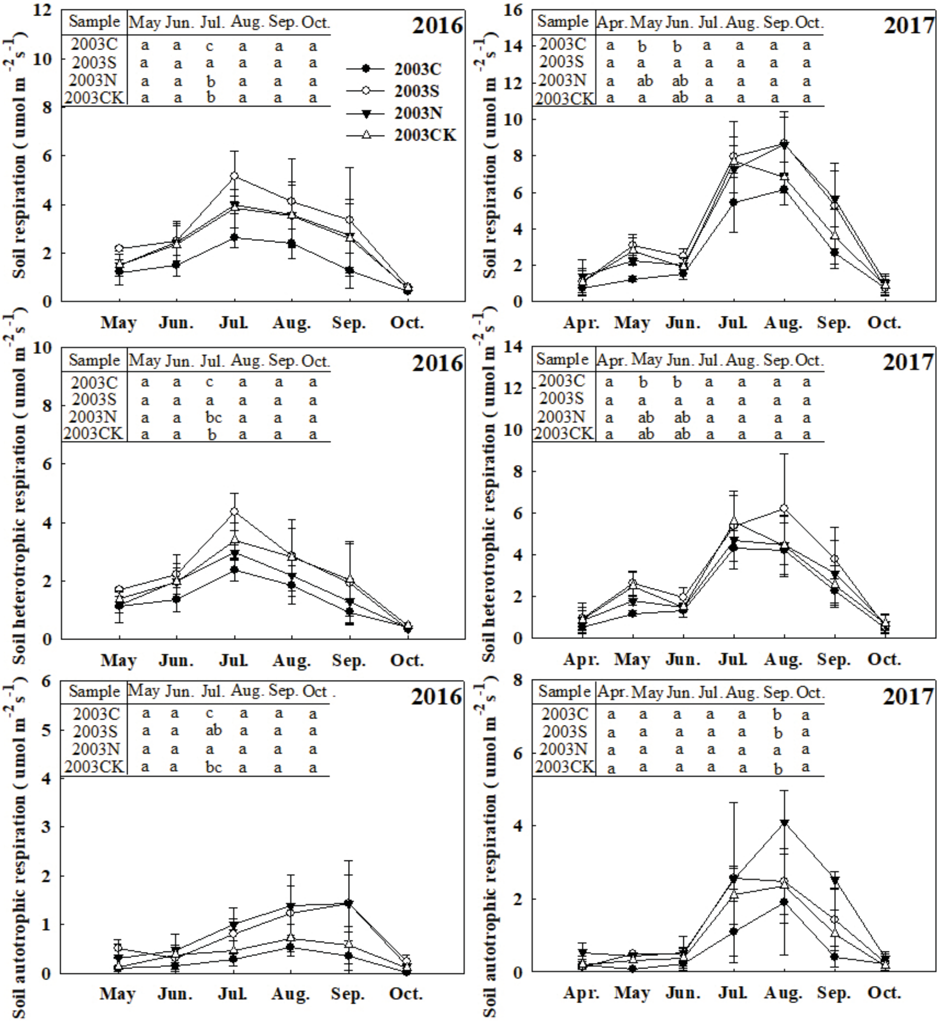


Figure 4: Monthly average soil respiration rate at four types of sample sites (see table 1). Letters (a, b, ab) show significant differences among sample sites in the same month and the same line (Tukey's HSD test), p-values were considered significant at a = 0.05.

Abbildung 4: Monatliche durchschnittliche Bodenatmungsrate an vier Arten von Probenstandorten (siehe Tabelle 1). Die Buchstaben (a, b, ab) zeigen signifikante Unterschiede bei Stichprobenstellen im selben Monat und in derselben Zeile (Tukeys HSD-Test), P-Werte bei α = 0.05 wurden als signifikant angesehen.

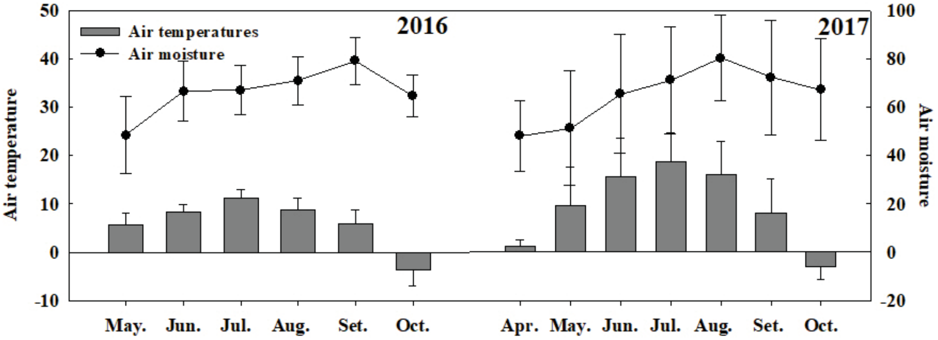


Figure 5: Monthly air temperature (°C) and air relative humidity (%) during the growing season in the research area.

Abbildung 5: Monatliche Lufttemperatur (°C) und relative Luftfeuchtigkeit (%) während der Vegetationsperiode im Forschungsgebiet.

Table 3: Annual-mean and range of total soil respiration (RS), heterotrophic soil respiration (RH) and autotropic soil respiration (RA) (μmol m^{-2} s^{-1}) in four types of sample sites. Values are annual means with standard deviations. Letters (a, b, ab) show significant differences among different sample sites in the same year and the same line. Letters (A, B) show significant differences in the same sample sites, and in different years (Tukey's HSD test), P-values were considered significant at α = 0.05. The orange values are the highest rates, mostly in the 2003S and 2003N plots; the blue values are the lowest, usually appeared in the 2003C plot.

Tabelle 3: Jahresmittelwert und Bereich von gesamter Bodenatmung (RS), heterotropher Bodenatmung (RH) und autotropher Bodenatmung (RA) (μmol m^{-2} s^{-1}) an vier Arten von Probenstellen. Die Werte sind Jahresmittelwerte mit Standardabweichungen. Die Buchstaben (a, b, ab) weisen erhebliche Unterschiede zwischen den verschiedenen Stichprobenstandorten im selben Jahr und in derselben Zeile auf. Die Buchstaben (A, B) zeigen signifikante Unterschiede zu denselben Stichprobenstandorten und in verschiedenen Jahren (Tukeys HSD-Test). Die P-Werte wurden bei α = 0.05 als signifikant angesehen. Die orange hervorgehobenen Werte zeigen die höchsten Raten hauptsächlich auf Plots mit selektiver bzw. ohne Nutzung. Die blau hervorgehobenen Werte sind die niedrigsten Raten auf Kahlschlagflächen.

Year	Soil respiration	2003C	2003S	2003N	2003CK
2016	RS	1.76±0.88Ab	3.36±1.89Aa	2.79±1.38Aab	2.71±1.40Aab
	RH	1.49±0.76Ab	2.54±1.51Aa	1.89±0.97Aab	2.26±1.17Aab
	RA	0.27±0.24Ab	0.82±0.65Aa	0.91±0.60Ba	0.45±0.29Bb
2017	RS	3.03±2.32Ab	4.71±3.34Aa	4.56±3.17Aab	3.94±2.78Aab
	RH	2.34±1.70Ab	3.41±2.84Aa	2.72±1.81Aab	2.84±1.97Aab
	RA	0.69±0.91Ab	1.30±1.18Aab	1.84±1.66Aa	1.10±1.05Ab

3.2 Effects of different salvage logging on the contribution of soil respiration

Contribution of soil respiration varied from month to month during the growing season (Figure 6). Generally, the contribution ratio of RH% was higher (> 50% in most months) than the ratio RA% (< 50%), as observed at the four types of soil conditions. The contribution of RA at 2003N plot maintained a high level during the growing season (higher than other sites). In 2016 and 2017, the maximum RA% of 2003C plot appeared in August; while in 2003S plot, the maximum RA% appeared in July 2016 and September 2017; in 2003N and 2003CK plot, the maximum RA% appeared in September 2016 and August 2017 respectively. RH% had different trends in each site; in 2016, except the 2003C plot, the RH% maximum value of the other three sample sites appeared in May, and the minimum value appeared in September; in 2017, except the 2003S plot the RH% maximum value of the other three sample sites appeared in May, and the minimum value appeared in August. The average contribution of RA over the growing season was less than 35% for all four types of sample plots (Table 4). The averaged RA% at 2003N plot was greater than that of 2003CK control plot. The RA% after salvage logging curtailed (i.e. 2003C < 2003S < 2003N in Table 4), and the greater the cutting intensity, the smaller the contribution ratio of RA. By analyzing the observed data, there was a significant difference in RA% between 2003C and 2003S, 2003C and 2003N respectively.

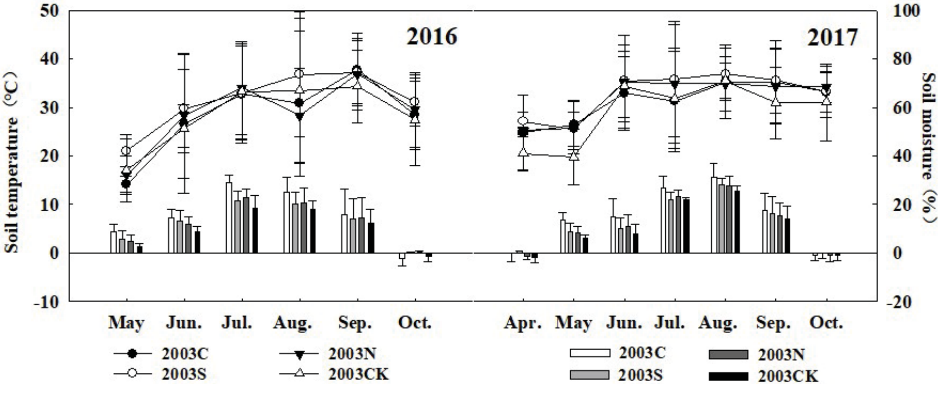


Figure 6: Monthly contribution ratio of soil respiration during growth season in the four types of sample sites.

Abbildung 6: Anteil der Bodenatmung pro Monat während der Vegetationsperiode in den vier Arten von Probenstandorten.

Table 4: Average contribution ratio of soil respiration RA and RH in four types of sample sites. Values are annual means with standard deviations. Letters (a, b, ab) show significant differences among salvage logging sample sites in the same line (Tukey's HSD test). P-values were considered significant at α = 0.05.

Tabelle 4: Anteil der Bodenatmung RA und RH in vier Arten von Probenstandorten. Die Werte sind Jahresmittelwerte mit Standardabweichungen. Die Buchstaben (a, b, ab) zeigen signifikante Unterschiede zwischen den Probenahmestellen für die Bergungsprotokollierung in derselben Linie (Tukey-HSD-Test). Die P-Werte wurden bei α = 0.05 als signifikant angesehen.

Sample plot Year		2003C	2003S	2003N	2003CK
2016	RA (%)	13.81±10.55b	25.92±14.51a	31.65±13.57a	16.19±6.08b
	RH (%)	86.12±10.53a	74.00±14.50b	68.38±13.64b	83.75±6.06a
2017	RA (%)	19.26±14.16b	24.91±12.28a	37.16±15.24a	24.47±11.69a
	RH (%)	80.82±14.11a	75.00±12.27b	62.88±15.22b	75.59±11.68b

3.3 Relationship between soil respiration and soil temperature-moisture

The monthly mean value of 10 cm soil temperature (T_{10}) varied within the growing season (Figure 7). T_{10} reached its peak in July 2016 and August 2017 respectively. The growing-season averaged value of T_{10} in the salvage logging plots (2003C and 2003S) was larger than that of the unburnt and uncut control plot (2003CK). It can be seen that fire disturbance caused soil temperature to rise, and the logging disturbance caused the further soil temperature rise, and the greater the cutting intensity, the greater the soil temperature rose.

The monthly mean value of 10 cm soil moisture (W_{10}) in the four types of sample plots had noticeable temporal variability within a season, and W_{10} in 2017 was higher than that in 2016 (Figure 7). The monthly mean value of W_{10} in 2016 peaked in September, with the minimum value in May. In 2017 it appeared to be the lowest and the highest in May and June respectively. During the two-year observation period, the minimum value of W_{10} appeared, probably due to the low precipitation in May, and because the vegetation in the region began to grow, the root system of vegetation absorbed a lot of soil water.

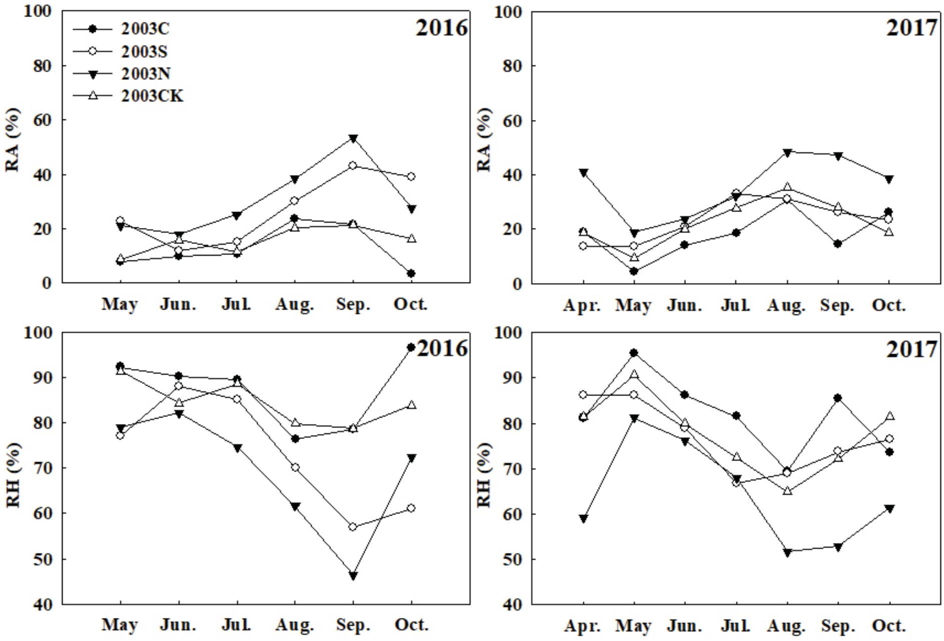


Figure 7: Monthly temperature and soil moisture at 10 cm depth, during the growing season, at four types of sample sites.

Abbildung 7: Monatliche Bodentemperatur und Bodenfeuchtigkeit in 10 cm Tiefe während der Vegetationsperiode an vier Arten von Probenstandorten.

The exponential regression provided a good description of the correlation between soil respiration (or each soil respiration component) with soil temperature (Table 5), except for RA at the 2003C plot, the RS, RH and RA at three salvage-logging plots and the control plot enhanced with the increase of T_{10}, and T_{10}, which had a significant exponential relationship with soil respiration or its components ($R^2 > 0.50$, $P < 0.01$ for two growing seasons). The RS and RH are well fitted with T10 at all four plots, but the RA was fitted relatively poor with T_{10} (R^2 of RH is between 0.64 ($P < 0.01$) and 0.82 ($P < 0.01$); R^2 of RA is between 0.13 ($P > 0.05$) and 0.59 ($P < 0.01$)). The correlation between RS and T_{10} in the burnt no-cut plot after 13 years of the fire disturbance was lower than that in the unburnt and uncut control plot (2003N $R^2 = 0.73$ vs. 2003CK $R^2 = 0.85$). Among the four types of sample plots, the 2003S plot had the highest fitting for RS or RH with T_{10} ($R^2 = 0.85$; $R^2 = 0.83$), the 2003CK plot had the maximum fitting for RA ($R^2 = 0.59$), and the 2003C plots had the lowest fitting for RS, RH, or RA ($R^2 = 0.53$; $R^2 = 0.64$; $R^2 = 0.17$). It can be seen that both the fire and harvest of fired trees affected the fitting of RS and soil temperature, making the correlation intensity varying.

The unitary quadratic regression model obtained to fit soil moisture W_{10}, and soil respiration components (Table 5) gave low coefficients of determination. There were no significant correlations between soil respiration (or its components) and W_{10} at the four types of sample sites ($R^2 < 0.2$ for most cases in Table 5, and $P > 0.05$), except for the 2003S sites RA and W10 ($R^2 = 0.26$, $P < 0.05$).

The interaction between soil temperature and soil moisture (as treated by the term of $W_{10} \times T_{10}$) and fitting degree with soil respiration rate and its components in the four sample sites were more suitable than single temperature factor or humidity factor; all regressions using equation (6) showed an extremely significant positive correlation ($R^2 < 0.55$; $P < 0.01$). Except for the 2003S plot RH, the fitting degree of soil respiration or its components and ($W_{10} \times T_{10}$) in the three types of burned wood management sample plot was lower than that in the 2003CK plot. The fitting degree was different in different types of burned wood management sample plot.

Table 5: Regression equations for soil respiration components with soil temperature (T_{10}) and soil moisture (W_{10}) for the four sample plots. R^2 is coefficient of determination.

Tabelle 5: Regressionsgleichungen für Bodenatmungskomponenten mit Bodentemperatur (T_{10}) und Bodenfeuchte (W_{10}) auf den vier Probeparzellen. R^2 ist das Bestimmtheitsmaß.

	Sample plot	Regression equation	R^2	P
T_{10}	2003C	$RS = 0.8593\ e^{0.1201\ T10}$	0.53	<0.01
		$RH = 0.6238\ e^{0.1093\ T10}$	0.64	<0.01
		$RA = 0.2193\ e^{0.0837\ T10}$	0.14	<0.05
	2003S	$RS = 1.2304\ e^{0.1401T10}$	0.85	<0.01
		$RH = 0.8846\ e^{0.1419T10}$	0.82	<0.01
		$RA = 0.3426\ e^{0.1361T10}$	0.55	<0.01
	2003N	$RS = 1.2544\ e^{0.1266T10}$	0.73	<0.01
		$RH = 0.8716\ e^{0.1158\ T10}$	0.72	<0.01
		$RA = 0.3952\ e^{0.1441T10}$	0.60	<0.01
	2003CK	$RS = 1.1359\ e^{0.1472T10}$	0.85	<0.01
		$RH = 0.9897\ e^{0.1318T10}$	0.79	<0.01
		$RA = 0.1782\ e^{0.1937T10}$	0.59	<0.01
W_{10}	2003C	$RS = 0.0006W_{10}^2-0.0320W_{10}+2.0414$	0.14	>0.05
		$RH = 0.0004W_{10}^2-0.0212W_{10}+1.7003$	0.10	>0.05
		$RA = 0.0002W_{10}^2-0.0108W_{10}+0.3411$	0.12	>0.05
	2003S	$RS = 0.0002W_{10}^2-0.2333W_{10}+9.3715$	0.17	>0.05
		$RH = 0.0016W_{10}^2-0.1870W_{10}+7.8197$	0.11	>0.05
		$RA = 0.0006W_{10}^2-0.0462W_{10}+1.5516$	0.26	<0.05
	2003N	$RS = 0.0001W_{10}^2-0.0329W_{10}+1.0962$	0.11	>0.05
		$RH = 0.0003W_{10}^2-0.0149W_{10}+1.8652$	0.10	>0.05
		$RA = -0.0002W_{10}^2+0.0478W_{10}-0.7691$	0.10	>0.05
	2003CK	$RS = 0.0003W_{10}^2+0.0108W_{10}+1.4923$	0.13	>0.05
		$RH = 0.0006W_{10}^2-0.0394W_{10}+2.6086$	0.13	>0.05
		$RA = 0.0003W_{10}^2+0.0502W_{10}-1.1163$	0.09	>0.05
$T_{10} * W_{10}$	2003C	$\ln(RS) = -0.3756+0.0877T_{10}-0.0007W_{10}+0.0005T_{10}W_{10}$	0.78	<0.01
		$\ln(RH) = -0.4438+0.0906T_{10}-0.0024W_{10}+0.0004T_{10}W_{10}$	0.80	<0.01
		$\ln(RA) = -3.4007+0.1191T_{10}+0.0089W_{10}+0.0006T_{10}W_{10}$	0.55	<0.01
	2003S	$\ln(RS) = 0.2549+0.1370T_{10}-0.0058W_{10}+0.0005T_{10}W_{10}$	0.86	<0.01
		$\ln(RH) = 0.1556+0.1472T_{10}-0.0092W_{10}+0.0004T_{10}W_{10}$	0.83	<0.01
		$\ln(RA) = -2.2442+0.1048T_{10}+0.0086W_{10}+0.0010T_{10}W_{10}$	0.59	<0.01
	2003N	$\ln(RS) = 0.1499+0.1248T_{10}-0.0025W_{10}+0.0003T_{10}W_{10}$	0.80	<0.01
		$\ln(RH) = -0.2361+0.1338T_{10}-0.0030W_{10}+0.0001T_{10}W_{10}$	0.77	<0.01
		$\ln(RA) = -1.2269+0.1136T_{10}-0.0005W_{10}+0.0006T_{10}W_{10}$	0.61	<0.01
	2003CK	$\ln(RS) = 0.3055+0.1495T_{10}-0.0067W_{10}+0.0004T_{10}W_{10}$	0.87	<0.01
		$\ln(RH) = 0.1215+0.1412T_{10}-0.0063W_{10}+0.0003T_{10}W_{10}$	0.82	<0.01
		$\ln(RA) =-1.6524+0.1878T_{10}-0.0066W_{10}+0.0004T_{10}W_{10}$	0.76	<0.01

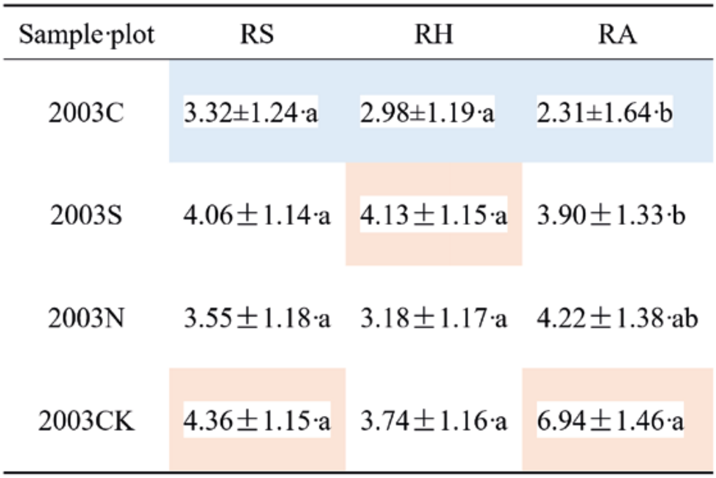
The three salvage-logging plots temperature sensitivity index Q_{10} for RS and RA were lower than that in 2003CK plot (Table 6). Among the four types of sample plots, the season-average value of Q_{10} for RS was the highest at 2003CK, showing a sensitivity trend as 2003CK > 2003S > 2003N > 2003C (Table 6); the average value of Q_{10} for RH was the largest at 2003S, showing a trend of 2003S > 2003CK > 2003N > 2003C; the Q_{10} for

RA was the largest at 2003CK, showing a trend of 2003CK > 2003N > 2003S > 2003C. These trends indicated that soil respiration rates became less sensitive to soil temperature after the fire and logging interferences, which is consistent with what had happened in the respiration-temperature correlation described above. On the other hand, a comparison of Q_{10} across respiration components showed that the Q_{10} values for RA in 2003CK and 2003N plots were larger than for RS or RH (showing RA-Q_{10} > RS-Q_{10} > RH-Q_{10}); the Q_{10} values for RH in 2003S were larger than for RS or RA (RH-Q_{10} > RS-Q_{10} > RA-Q_{10}), the Q_{10} values for RS in 2003C were larger than for RH or RA (RS-Q_{10} > RH-Q_{10} > RA-Q_{10}).

These patterns' correlation and sensitivity showed that fire disturbance reduced the sensitivity of soil respiration and its components to soil temperature; and salvage logging also reduced the sensitivity, with the clear-cutting mostly reduced the sensitivity of soil autotrophic ($P < 0.05$). While Q_{10} in selective-cutting 2003S plot differed a little (only reduced from 4.36 to 4.05): less decreased in 2003N or 2003C for RS. However, Q_{10} in the selective-cutting 2003S plot became larger than in the 2003CK for RH (from 3.74 to 4.13).

Table 6: Soil respiration component Q_{10} values in the growing season at four types of sample sites. Highlighted blue indicated the lowest and orange the highest values, respectively. Values are annual means with standard deviations. Letters (a, b, ab) show significant differences among salvage logging sample sites in the same line (Tukey's HSD test). P-values were considered significant at α = 0.05.

Tabelle 6: Q_{10}-Werte der Bodenatmungskomponenten in der Vegetationsperiode an vier Arten von Probenstandorten. Blau hervorgehoben zeigt die niedrigsten und orange die höchsten Werte an. Die Werte sind Jahresmittelwerte mit Standardabweichungen. Die Buchstaben (a, b, ab) zeigen signifikante Unterschiede zwischen den Probenahmestellen in derselben Linie (Tukey-HSD-Test). Die P-Werte wurden bei α = 0.05 als signifikant angesehen.



Sample plot	RS	RH	RA
2003C	3.32±1.24 a	2.98±1.19 a	2.31±1.64 b
2003S	4.06±1.14 a	4.13±1.15 a	3.90±1.33 b
2003N	3.55±1.18 a	3.18±1.17 a	4.22±1.38 ab
2003CK	4.36±1.15 a	3.74±1.16 a	6.94±1.46 a

4. Discussion

4.1 Fire disturbance on soil respiration and its components

The study indicated that the effects of fire disturbance on soil respiration varied with site location or condition for a given region. Hu *et al*. (2017) measured the effects of different fire intensity on soil respiration with the *Larix gmelinii* forest in another area of the same Daxing'anling mountains, where the fire broke out in 2006, with soil respiration monitored from 2010 to 2012. They found that both the soil respiration rate and soil autotrophic respiration in the burned sample plots were lower than those in the unburned plot. This finding is different from the results obtained in the study (the soil respiration and autotrophic respiration increased). Their research area located in the southeastern foothill of the Daxing'anling mountains, which was a temperate continental monsoon climate with no permafrost, and in which herbs and shrubs were abundant compared with the research area (northern Daxing'anling, permafrost), and the two study areas were 210 km apart. Fire changed soil structure and properties, which affected survival quantity and living environment of microorganisms (Holden *et al*., 2015), resulting in the RH of burnt sample plots, after 13 years since the fire event, being smaller than the unburnt control sample plot (i.e. smaller at 2003N than at 2003CK). At the same time, the fire changed the growth environment and mechanism of trees, which affected the root respiration of fired trees and understory vegetation (Bryanin and Makoto 2017). After 13 years from fire disturbance, the vegetation restoration was good, the number of tree regeneration increased, and the biomass of understory vegetation was higher, which promoted the soil autotrophic respiration (Table 2). RA at the burned plots (2003N) became higher than that of the unburnt control plot (2003CK).

The contribution ratio of heterotrophic respiration was higher than the ratio of autotrophic respiration (RH% > RA%), which is similar to the previous studies (e.g. Heim *et al*., 2015; Lin *et al*., 1999). The RA% in the burnt plots was more significant than that in the no-fire plot. However, the salvage logging intensity decreased it: the higher the cutting intensity, the smaller the ratio. The reason may because that fire reduced the amount and activity of soil microorganisms (Wang *et al*., 2012), and changed the growth environment and growth mechanism at the same time, thus caused the RH to weaken and RA to increase.

Potential response of soil respiration to changes in environmental factors can be separated into the response of autotrophic and heterotrophic respiration, as their responses to soil temperature may vary (Archmiller and Samuelson, 2016). At research sites, the regression fitting strength of soil respiration (or its components) with soil temperature is high, similar to the results of Jian *et al*. (2019). The study provided a useful addition of the respiration-temperature relation for cold, permafrost regions, and confirmed the sensitive response of soil autotrophic respiration to temperature change. As found by others (Lu *et al*., 2010, Epron *et al*., 2001), the autotrophic sensitivity Q_{10} value (6.94) of the unburnt and uncut sample plot was higher than the RH's Q_{10} value (3.74), supporting that autotrophic respiration is more sensitive than heterotrophic respiration in the *Larix gmelinii* forest in the cold temperate zone of a permafrost region. The Q_{10} values for all RS, RA and RH at the burnt without cut plot were lower than that of the unburnt and uncut control plot, which suggested that the fire disturbance reduced the sensitivity of soil respiration to temperature, probably because burnt plots had thinner litter layer and weaker decomposition ability (Davidson *et al.*, 2006).

4.2 Difference of soil respiration and its components among different salvage-logging management method

The results indicated a contrasting effect between the selective-cutting (promoting soil respiration) and the clear-cutting (lowering soil respiration). The findings of positive effect in selective-cutting (increasing soil respiration rates) observation here is similar to Concilio *et al.* (2005) for burnt and thinned mixed-conifer and hardwood forests. Some other studies could support the negative or lowering effect of clear-cutting at the site, e.g., López-Serrano *et al.* (2016) for a Mediterranean mixed forest. However, some other studies have shown contrarily (e.g. Parro *et al.*, 2019) on burned and clear-cutting plots compared to burned and uncleared plots, showing no differences in respiration rates. Ma *et al.* (2013) suggested that felling had no significant effects on cumulative annual soil respiration releases, mainly because root respiration usually stopped shortly after tree harvesting, resulting in a sudden decrease in soil autotrophic respiration. However, the decomposed dead roots increased the number and activity of microorganisms, which could counteract the decline in root respiration. At the same time, the newly increased growth of herbaceous and other plant roots within the sample plots may offset the soil autotrophic respiration reduction.

Salvage logging affected the further soil respiration and changed the effects or patterns which were initially formulated by the fire event. Moderate logging (selective-cutting 2003S) was benefited to the vegetation renewal and soil microbial activities in the fired area, increasing the RH against other two logging practices (i.e. giving an RH rate pattern of 2003S > 2003N > 2003C). It is observed that the minimums of RS, RH and RA were all found in the clear-cutting (2003C) plot investigated as the high-intensity cutting has a lower effect on soil respiration and its components, because the high-intensity cutting of burned wood changed the aboveground vegetation composition and biomass (Takada *et al.*, 2015). Most aboveground vegetation was new after the burned wood cleared, the RA rate became weak, and the underground microbial amount was reduced, which led to the soil respiration components at the 2003C plot to became lower compared to the other plots.

The changes in contribution ratios could also be explained by the changes in soil temperature and vegetation amount. Nakane *et al.* (1996) suggested that the root respiration was strictly related to the amount of vegetation on the ground, accounting for about 30% of total respiration (which is comparable to the ratios of the sites). Lin *et al*. (1999) found that the increase in temperature would increase the contribution rate of soil autotrophic respiration. The soil temperature at depth 10 cm at salvage-logging plots was higher than at the no-fire no-cut control plot, which was caused by the changed tree growth environment due to fire. As a result, the vegetation root respiration rate (i.e. soil autotrophic respiration contribution ratio) increased after the fire. However, the salvage-logging management reduced the biomass of trees and changed the forest canopy density. The higher the cutting intensity, the smaller the proportion of soil autotrophic respiration would be at the fired plots (as shown by 2003N > 2003S > 2003C).

Both fire and logging increase soil temperature, and the incremental temperature at the cut plot after a fire is higher than that at the burnt no-cut plot (Concilio *et al*., 2005). The study provided another confirmation. The sensitivity also differed from salvage logging methods, as shown a greater Q_{10} at the 2003S plot than at 2003N or 2003C plot. Cutting has a substantial impact on the biomass of soil roots. After ten years from the salvage-logging management, the clear cutting (2003C) reduced the number of mature trees. Therefore, the sensitivity of autotrophic respiration to temperature may be related to the number of roots biomass of mature trees. Soil moisture may not be a key factor affecting the soil respiration of the *Larix gmelinii* forest in the permafrost region, In terms of the experiment, there were lack of no noticeable changes in soil moisture among the three salvage-logging management plots and the unburnt and uncut control plot. Holden *et al*. (2015) found no significant differences in soil moisture between fired and unfired plots, which was consistent with the research findings.

5. Conclusions

After thirteen years fire disturbance and ten years salvage-logging management at a cold and permafrost area in the Daxing'anling mountains, the impact of fire and logging on soil respiration of the studied area still existed. Forest fire increased soil autotrophic respiration but decreasing soil heterotrophic respiration, resulting in a slightly increased total soil respiration compared to the unburnt and uncut control plot. This research will report in the first time that: the selective-cutting of burnt tree enhanced the soil respiration and its components, producing most considerable respiration rates at the selective-cutting plot among different cutting intensities. In contrast, clear-cutting weakened soil respiration and its components produced the lowest respiration rates. The proportion of heterotrophic soil respiration to soil respiration was much more significant than the ratio of autotrophic respiration. The fire disturbance increased the proportion of soil autotrophic respiration, but the salvage logging reduced it, and the higher the cutting intensity, the lower the contribution ratio. The logging of burnt trees increased soil temperature, and the greater the cutting intensity, the higher the temperature would be. Although soil respiration and its components were positively correlated to soil temperature in all plots, both the fire and logging interferences had reduced the sensitivity of soil respiration to soil temperature. There were no significant correlations between soil respiration and soil moisture in the studied forest. The results suggested clearly that the direction (positive or negative) and extent of the effects on soil respiration could be quite different between fire disturbance and post-fire logging, and the effects can differ significantly from logging methods. Based on current analysis of soil respiration data, we prefer not to conduct burnt wood logging. However, soil respiration is the only index of soil and forest ecosystem, scientifically sound management policy for fired forest may not be recommended without considering all ecological and forestry factors. More studies and experiments are required.

Author's contributions

M. Zhou and Z. Wang initiated the research plan; Z. Wang synthesized the field work and results; Z. Wang and H. Yao wrote the manuscript; D. Wang conducted some statistical work and helped writing the manuscript. P. Zhao helped field work; A. James helped writing the manuscript.

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Conflict of interest

None declared.

Appendix

Vegetation investigation

Identifying regenerated trees was based on the tree height. The forest fire broke out in 2003 and a vegetation survey was conducted in 2016. The regenerated trees were maximum 13 years old and the height of regeneration of *Larix gmelinii* and *Betula platyphylla* was no more than 2.5 m, which made it easy to identify them. The post-fire logging did not prefer particular tree species, but removed trees according to the degree of burning.

Five 5 m× 5 m quadrats were set at the four corners and the center of each sample plot respectively to investigate shrub indicators. Five 1 m×1 m quadrats were randomly set in each shrub quadrat to investigate herb indicators. Species, height, number of plant clusters and coverage were investigated in the shrub and herb quadrats. In order to preserve the integrity of the plot, the shrub was sampled by the standard branch method. According to the survey data of each shrub in the sample plot, the plants in whole sample plot were divided into three grades respectively according to the arithmetic mean of three indexes - the plant height, ground diameter and the sum of height and ground diameter, then three shrubs were selected for each grade (Liu, 1994). The biomass of aboveground shrubs was determined by Monsi layer cutting method (Monsi, 2005). The whole harvest method will be applied, if a shrub were not meet the selection criteria for the standard wood. Herbs were collected by total harvest method. Taking three litter quadrats of 0.2 m × 0.2 m randomly and setting in each plot, including deciduous grass and branches with diameters less than 2 cm, excepting for fallen wood and branches with diameters greater than 2 cm. We measured the fresh mass after sampling shrubs, herbs and litter, then brought the material back to the laboratory and dried at 80 °C until the mass was constant and weighed again. The biomass per unit area and litter amount of each shrub and herb were estimated according to the quadrat mean value.

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