

RESEARCH ARTICLE

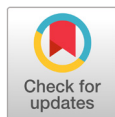
Effects of Thinning Intensity on Ectomycorrhizal Fungal Communities in *Pinus densiflora* Plantations

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ABSTRACT

Thinning is widely used to regulate tree growth and stand structure. However, its impact on belowground ectomycorrhizal (ECM) fungi in Korean pine forests remains insufficiently documented. Therefore, in this study, we investigated the effects of thinning intensity on ECM fungal community composition and diversity in *Pinus densiflora* plantations. The ECM root tips were identified using morphological criteria and DNA sequencing. Across intensities, 23–35 ECM fungal species were recorded per plot, and only three taxa, *Amanita pantherina*, *Lactarius* sp., and *Russula mairei*, occurred consistently across all treatments. Non-metric multidimensional scaling indicated a distinct community composition in the control group relative to those in the thinned plots; communities partially overlapped but shifted along the thinning-intensity gradient. These results suggest that thinning intensity influences the ECM fungal community and should be considered when planning forest management that accounts for belowground biodiversity.



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Keywords: Community structure, Ectomycorrhizal fungi, *Pinus densiflora*, Thinning

INTRODUCTION

Ectomycorrhizal (ECM) fungi play an essential role in forest ecosystems by forming mutualistic associations with plant roots [1]. They produce a fungal mantle that covers the root surface and extend their hyphae into the soil, improving the host's uptake of nutrients, such as nitrogen and phosphorus. Within the root cortex, fungal hyphae develop a network-like structure known as the "Hartig net," which mediates the exchange of nutrients between the host and fungus [2]. Through this relationship, host plants transfer a substantial portion of their photosynthetic carbon (~22% of net primary production) to their fungal partner [3]. In return, ECM fungi enhance host resistance to drought, soil acidification, and root pathogens, thereby contributing to plant growth and forest stability [4,5].

Pinus densiflora Siebold et Zucc. is a major ECM tree species that is widely distributed across East Asia, including Korea, Japan, and China. In Korea, *P. densiflora* plantations play a central role in reforestation, timber production, and the cultivation of economically valuable non-timber products such as *Tricholoma matsutake* (S.Ito & Imai) Singer [6]. However, the dominance of monospecific pine stands has been associated with a decline in biodiversity and the weakening of ecosystem functions [7]. In managed pine stands, thinning is often performed to mitigate the negative effects of high stand densities. Thinning can reduce density-driven competition and improve understory diversity, light availability, and soil nutrient cycling, thereby enhancing ecosystem functions. These ecological benefits justify using thinning as a management tool to improve biodiversity and maintain forest health.

Various ECM fungi, including *Russula*, *Lactarius*, *Cortinarius*, and *Suillus*, have been reported in *P. densiflora* forests in Korea [8]. The composition and diversity of ECM fungal communities vary depending on host specificity and environmental factors, such as soil chemistry, microclimate, and forest management. Among these factors, forest disturbances strongly influence ECM fungal community dynamics. For example, *Suillus* species commonly dominate the early successional stages after thinning or fire, whereas *Russula* and *Cortinarius* species, which are adapted to mature forest conditions, tend to prevail in later stages [9].

Thinning is a key silvicultural practice that is applied to reduce stand density and promote the growth of healthy trees. It improves light penetration, soil moisture, and nutrient redistribution, enhancing forest productivity and stability [10,11]. However, thinning is also a form of anthropogenic disturbance that may affect belowground biotic communities, including that of ECM fungi, which are crucial for forest ecosystem functioning. Despite its ecological importance, the influence of thinning intensity on ECM fungal communities in Korean *P. densiflora* plantations remains poorly understood. Therefore, in this study, we investigated the effects of thinning intensity on the composition and diversity of ECM fungal communities in *P. densiflora* plantations.

MATERIALS AND METHODS

Study site and thinning treatments

Sampling was conducted in a *P. densiflora* plantation on Mt. Chilbo, Byeonggok-myeon, Yeongdeok-gun, Gyeongsangbuk-do, Korea (36°38'N, 129°22'E). The stand (~17.5 ha) was thinned in 2008. Within the same stand, an unthinned control plot and five thinned plots adjacent to the control plot were delineated (Table 1). Three plots underwent low thinning (from below) at different intensities: light (34%), moderate (45%), and heavy (60%). Two plots underwent moderate-intensity thinning using different thinning methods: selection thinning (43%) and mechanical thinning (46%).

Table 1. Introduction of collection sites

Collection site type	Coordinate	No. of plots (No. of samples)	Intensity of thinning (%)
Control site	36° 38'05.7"N 129° 22'10.6"E	3(15)	0
Thinning site			
Low thinning site			
Light thinning site	36° 37'54.5"N 129° 22'12.7"E	3(15)	34
Moderate thinning site	36° 37'59.4"N 129° 22'10.7"E	3(15)	45
Heavy thinning site	36° 38'07.0"N 129° 22'14.5"E	3(15)	60
Selection thinning site	36° 38'10.7"N 129° 22'15.7"E	3(15)	43
Mechanical thinning site	36° 37'49.1"N 129° 22'14.1"E	3(15)	46

Soil and root sampling

To collect ECM material, soils were sampled in March 2016. In the unthinned control plot and each of the five thinned plots, three 10 m × 10 m quadrats were established and overlaid with a 1 m grid (100 cells). Using simple random sampling, five soil cores (100 mL each) were collected per quadrat using a soil sampler (Heungjin Co., Gimpo, Korea), yielding 90 soil samples in total (6 plots × 3 quadrats × 5 cores).

Fine roots recovered from the soil were rinsed with distilled water, and ECM colonization was confirmed under a dissecting microscope based on the presence of a fungal mantle. The ECM root tips were then assigned to morphotypes based on standard criteria, including mantle color and texture, tip morphology and branching pattern, and the presence or absence of emanating hyphae and rhizomorphs [12].

Molecular identification of ECM morphotypes

The ECM morphotypes (root tips) were identified using a molecular approach. Root tips were surface-sterilized with 30% H₂O₂ and finely homogenized, and total genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The nuclear ribosomal internal transcribed spacer (ITS) region (ITS1–5.8S–ITS2), a standard fungal barcode, was amplified with the fungus-specific primer ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') and the universal primer ITS4 (5'-TCCTCCGCTTATTGATATGC-3') [13]. We performed PCR amplification under the following conditions: an initial denaturation at 94 °C for 3 min; 35 cycles of 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 90 s; and a final extension at 72 °C for 5 min. The PCR products were purified and Sanger sequenced by SolGent (Daejeon, Korea). The resulting ITS sequences were queried using BLASTn against the National Center for Biotechnology Information nucleotide database to identify the closest matches, and species-level assignments were further verified through phylogenetic analyses conducted using MEGA software [14] (Table S1).

Community structure analysis

The composition of the ECM fungal community was examined in the unthinned and thinned plots. The Shannon diversity index [15], evenness [16], and species richness were calculated based on the number of species, and the number of ECM root tips was calculated based on the root-tip counts per species and total root-tip abundance using MVSP (Kovach Computing Services, Pentreath, UK). The relative abundance of each species was also determined. Similarity in ECM fungal community structure was assessed using non-metric multidimensional scaling (NMDS) with the Sørensen (Bray–Curtis) distance measure in PC-ORD 6 (Wild Blueberry Media, Corvallis, OR, USA). To evaluate the effects of thinning intensity, ECM fungal communities were compared between the unthinned control and low-thinning treatments with different thinning intensities using one-way analysis of variance (ANOVA) in SPSS 12 (SPSS Inc., Chicago, IL, USA). To assess the effects of thinning method, ECM fungal community characteristics were compared between the unthinned control and the moderate-thinning treatment that differed only in thinning method (low thinning, selection thinning, and mechanical thinning).

RESULTS AND DISCUSSION

The ECM fungi from the control and treatment plots were identified through morphotyping and molecular analyses. In the unthinned plot, 23 species were recorded. Among the low-thinning treatments, 22 species occurred under light thinning, 32 species under moderate thinning, and 27 species under heavy thinning (Table S1). At the same moderate-thinning intensity, 35 species were found in the selection-thinning plots and 29 species were found in the mechanical-thinning plots. Only three taxa, *Amanita pantherina*, *Lactarius* sp., and *Russula mairei*, occurred in all plots, whereas overall, the species composition differed among treatments, indicating high turnover.

The dominant taxa varied across plots. For example, *Lactarius* sp.1 had the highest relative abundance in the moderate-thinning plots (52.26%), whereas *Clavulina* sp.1 was the most abundant in the heavy-thinning plots (10.96%). Meanwhile, *Tomentella* spp. and *Russula mairei* occurred frequently in several plots, with *R. mairei* reaching its highest abundance under moderate thinning (20.80%). These dominant species differed among the treatments, contributing to high turnover in ECM fungal community structure (Table S1).

We performed NMDS to assess among-plot differences in the ECM fungal community composition (Fig. 1). The ECM fungal communities differed with thinning intensity, and the unthinned control plot was clearly distinct from the thinned plots along Axis 1. Although there was some overlap among treatments, the ordination indicated a gradual shift in community structure along the thinning-intensity gradient. The mechanically thinned plot showed low within-group dispersion and was separated from the other treatments, whereas the selection-thinned plot had more overlap with the control. In contrast, the moderately thinned plots exhibited greater within-group dispersion in the ordination, likely reflecting the increased microhabitat heterogeneity created by partial canopy opening. Such heterogeneity in soil moisture, litter input, and root conditions could lead to more variable ECM assemblages among the plots in this treatment. This broader range of assemblages under moderate thinning is consistent with the higher alpha diversity (Fig.

2), indicating that intermediate levels of disturbance create favorable conditions for diverse ECM fungal communities. Overall, thinning was associated with a directional shift in the ECM fungal community composition, whereas the unthinned stand retained a composition characteristic of undisturbed conditions.

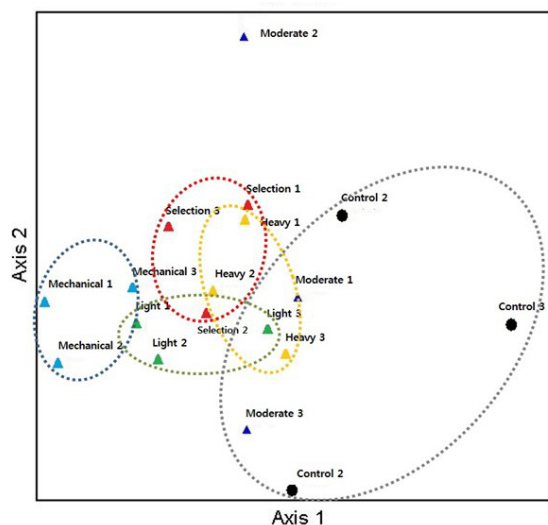


Fig. 1. Non-metric multidimensional scaling (NMDS) ordination of ectomycorrhizal (ECM) fungal communities across control and thinning treatments (Sørensen/Bray–Curtis). Points are plots; dotted envelopes indicate groups. Intensity: green (light), blue (moderate), yellow (heavy). Method at moderate intensity: cyan (mechanical), red (selection). Control = black.

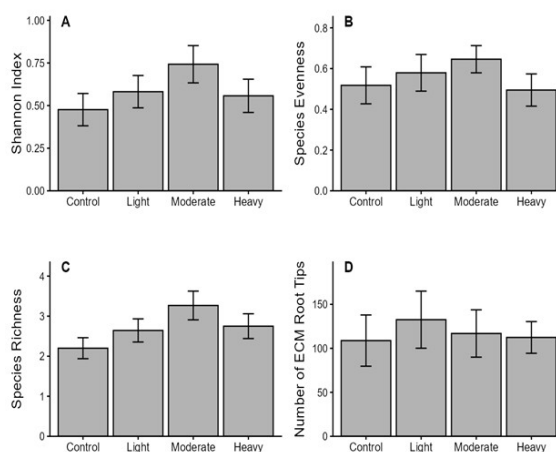


Fig. 2. Effects of thinning intensity on ectomycorrhizal (ECM) fungal community. A: Shannon diversity index, B: Evenness index, C: Species richness of ECM morphotypes, and D: Number of ECM root tips across four thinning intensities. Bars represent means \pm standard errors of three plots per treatment.

One-way ANOVA (Fig. 2) indicated no statistically significant differences between the control and thinned plots in terms of alpha-diversity metrics. Shannon diversity was the lowest under the control and increased with thinning, with the highest diversity under moderate thinning. Evenness showed a similar pattern, peaking under moderate thinning, and species richness followed the same trend. Although these differences were not statistically significant, consistent directional trends suggest that moderate thinning

may enhance ECM fungal diversity. In contrast, the abundance of ECM root tips was the highest under light thinning, implying that low-level canopy opening may increase the abundance of colonized tips without necessarily maximizing taxonomic diversity. Overall, compared with the control, thinning tended to increase species diversity, richness, and colonization metrics, with the strongest trends generally observed under moderate-intensity thinning. These results are consistent with the intermediate disturbance hypothesis, which proposes that moderate disturbance reduces belowground competition and increases environmental heterogeneity, thereby promoting higher diversity of ECM fungi [17,18]. From a forest management perspective, this suggests the need for a balanced approach between “non-intervention conservation” for protected areas and “intensive disturbance” for timber production. In particular, moderate thinning may serve as an effective strategy for maintaining forest health while supporting ECM diversity.

When thinning methods were compared under moderate-intensity thinning (Fig. 3), selection thinning resulted in the highest species diversity and evenness, whereas mechanical thinning produced the greatest number of ECM root tips. These results indicate that selection thinning favors a more balanced ECM fungal community, whereas mechanical thinning promotes root-tip proliferation, likely reflecting differences in soil disturbance and resource availability. Both thinning methods differed significantly from the control in several metrics (e.g., richness and tip abundance), suggesting that stand structural changes associated with thinning can modulate ECM assemblages beyond the effect of intensity alone. Because the thinning methods were sampled at a single intensity, these contrasts should be interpreted with caution.

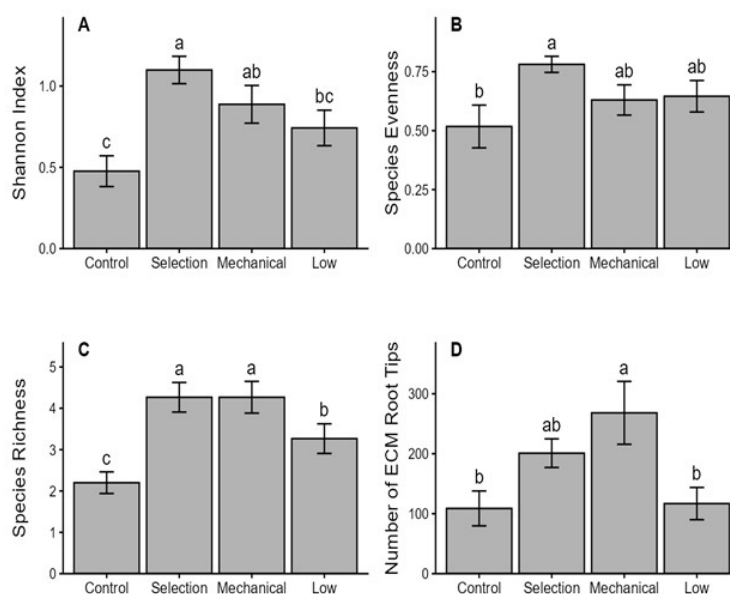


Fig. 3. Effects of thinning method on ectomycorrhizal (ECM) fungal community. A: Shannon diversity index; B: Evenness index; C: Species richness of ECM morphotypes; D: Number of ECM root tips across four thinning intensities. Bars represent means \pm standard errors of three plots per treatment. Different letters above the bars indicate statistically significant differences among thinning methods (Fisher's least significant difference test, $P < 0.05$).

Ecologically, thinning influences not only tree growth but also belowground fungal diversity, which is integral to long-term forest stability and ecosystem functioning [9,19]. From a management perspective, our results suggest that moderate thinning intensity and, where suitable, selection thinning, sustain forest health while supporting ECM diversity. Because the thinning methods were evaluated at only one intensity, the experimental design was unbalanced with respect to the operation type. Future studies should incorporate factorial designs spanning multiple thinning intensities and methods as well as temporal resampling to assess the persistence and generality of these patterns.

The combined evidence indicates that thinning alters ECM fungal community structure by changing both the host environment (stand density and canopy conditions) and abiotic conditions (light, soil moisture, and soil nutrients), which in turn influence enzyme expression, nutrient-uptake strategies, and interactions with hosts and other soil microbes. The outcomes of thinning vary across treatments [20] and do not act uniformly on all species within ECM fungal communities [21]; species-specific responses lead to shifts in relative abundance and changes in dominant taxa [22,23]. Taken together, varying thinning intensities and methods differentially affect the ecology of particular ECM species, thereby restructuring the community composition. We anticipate that this study will serve as a baseline for planned thinning programs in Korea and support strategies for establishing healthy forest stands.

CONFLICT OF INTEREST

No conflict of interest was reported by the authors.

ACKNOWLEDGEMENTS

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Table S1. Relative abundances (%) of ectomycorrhizal fungal taxa across thinning treatments

Species	Closest GenBank sequences		Control	Thinning intensity ^a			Thinning method ^b	
	Accession No.	Similarity (%)		Light	Moderate	Heavy	Selection	Mechanical
<i>Amanita citrina</i>	KP004945	100	-	4.26	-	-	1.06	-
<i>Amanita flavipes</i>	AB015696	99	-	-	-	-	-	0.40
<i>Amanita fritillaria</i>	KM052533	97	-	-	-	-	0.07	-
<i>Amanita griseofolia</i>	FJ441043	98	-	-	-	0.95	-	-
<i>Amanita pantherina</i>	AB080977	99	5.70	1.24	2.51	0.89	0.56	1.07
<i>Amanita</i> sp.	AB015682	91	0.12	-	-	0.44	-	-
<i>Amphinema</i> sp.	JN943925	99	0.67	-	-	4.34	0.46	-
<i>Boletus reticulatus</i>	AB821462	99	-	-	0.86	-	-	0.75
<i>Boletus</i> sp.	FJ480441	93	-	-	-	-	-	0.02
<i>Cantharellus</i> sp.1	HQ416694	93	-	-	0.29	-	-	-
<i>Cantharellus</i> sp.2	KF692074	94	-	0.32	-	-	0.36	-
<i>Cenococcum geophilum</i>	DQ474328	99	-	-	1.25	-	-	3.51
<i>Chroogomphus confusus</i>	EF423623	97	-	-	-	-	-	2.16
<i>Clavulina</i> sp.1	KP403070	97	5.15	1.35	11.69	10.96	10.45	-
<i>Clavulina</i> sp.2	KR673708	99	-	-	0.63	-	-	-
<i>Cortinarius</i> sp.1	FJ039662	93	-	-	-	0.39	-	0.22
<i>Cortinarius</i> sp.2	FJ717549	95	-	-	-	-	-	1.42
<i>Cortinarius</i> sp.3	JN847491	88	-	0.11	-	-	-	-
<i>Cortinarius</i> sp.4	JQ991698	91	-	-	-	0.22	-	-
<i>Cortinarius</i> sp.5	DQ481687	90	-	-	-	-	0.50	-
<i>Cortinarius</i> sp.6	FJ152507	93	-	-	-	-	-	0.80
<i>Cortinarius</i> sp.7	FJ717574	88	-	-	-	-	0.53	-
<i>Craterellus</i> sp.	AY082606	96	-	-	-	-	-	11.98
<i>Entoloma</i> sp.1	KJ705160	89	-	0.38	-	-	1.66	-
<i>Entoloma</i> sp.2	LN850590	89	-	-	-	-	0.10	-
<i>Entoloma</i> sp.3	LN850570	92	0.92	-	-	-	-	-
<i>Entoloma</i> sp.5	AB848485	94	15.01	-	2.85	0.22	-	-
<i>Gomphidius</i> sp.1	AF205638	93	-	-	-	3.34	2.72	-
<i>Helotiales</i> sp.1	JF273525	100	1.47	0.22	2.00	0.33	2.59	-
<i>Helotiales</i> sp.2	JF273525	99	-	4.90	0.63	0.28	1.79	5.99
<i>Helotiales</i> sp.3	FJ827169	99	-	-	0.80	0.17	1.13	2.31
<i>Helotiales</i> sp.4	FJ440902	99	-	-	-	-	5.34	0.82
<i>Helotiales</i> sp.5	FJ827166	99	-	-	-	-	-	0.40
<i>Hydnellum</i> sp.	JN135177	86	-	-	-	-	-	5.82
<i>Hydnum</i> sp.	AB906676	99	-	-	-	-	-	3.80
<i>Inocybe</i> sp.1	AM882802	96	-	-	-	-	1.26	-
<i>Inocybe</i> sp.2	JF273522	99	-	-	1.25	-	-	-
<i>Lactarius hatsudake</i>	KF432967	99	3.80	-	2.28	-	1.66	-
<i>Lactarius</i> sp.1	AB972830	99	2.39	52.26	6.67	16.57	17.92	40.35
<i>Lactarius</i> sp.2	FJ596848	95	-	0.65	2.11	12.07	4.01	-
<i>Meliniomyces</i> sp.	FN565279	92	-	-	-	-	2.19	-

Table S1. Relative abundances (%) of ectomycorrhizal fungal taxa across thinning treatments(continued)

Species	Closest GenBank sequences		Control	Thinning intensity ^a			Thinning method ^b	
	Accession No.	Similarity (%)		Light	Moderate	Heavy	Selection	Mechanical
<i>Rhizopogon</i> sp.	AB253521	94	-	-	1.03	2.67	23.76	-
<i>Russula cerolens</i>	JX434674	99	-	-	0.11	-	-	-
<i>Russula mairei</i>	KF002786	99	2.39	3.72	3.31	20.80	3.42	0.52
<i>Russula nigricans</i>	EU819428	98	-	3.23	-	-	-	-
<i>Russula</i> sp.1	KF359616	92	-	-	8.44	-	-	1.54
<i>Russula</i> sp.2	JF908661	96	-	-	-	-	-	0.10
<i>Russula</i> sp.3	KF386752	91	27.94	-	1.14	-	-	-
<i>Russula</i> sp.4	KM502971	100	-	0.05	-	0.28	-	-
<i>Russula</i> sp.5	JN129410	95	7.41	-	-	-	-	-
<i>Russula</i> sp.6	LC029801	99	-	3.77	-	-	-	-
<i>Russula</i> sp.7	AB972834	99	-	-	0.68	-	-	-
<i>Russula</i> sp.8	GQ344560	99	-	-	18.20	-	-	-
<i>Russula</i> sp.9	HE814170	96	-	-	0.34	-	-	-
<i>Russula</i> sp.10	AB848564	86	-	-	-	-	-	0.25
<i>Russula vesca</i>	HM189953	98	-	-	1.60	-	-	-
<i>Sebacina candida</i>	KP783467	99	-	-	-	-	1.03	-
<i>Sebacina dimitica</i>	KF061273	97	-	-	-	-	0.60	-
<i>Sebacina</i> sp.1	JQ347197	98	0.37	-	-	-	-	-
<i>Sebacina</i> sp.2	LC035279	96	-	-	-	1.84	0.43	-
<i>Sebacina</i> sp.3	JQ347200	98	-	-	-	-	-	2.01
<i>Sistotrema</i> sp.	KM402986	92	-	4.74	-	-	1.53	-
<i>Suillus bovinus</i>	FJ481028	99	0.98	3.02	1.08	-	1.99	-
<i>Suillus</i> sp.	AB284436	89	-	-	-	-	-	0.02
<i>Thelephora</i> sp.1	AJ889980	94	-	-	-	-	1.39	-
<i>Thelephora</i> sp.2	JF506814	99	-	9.00	6.22	7.90	5.24	1.79
<i>Tomentella ramosissima</i>	JX630402	97	-	-	1.94	-	0.10	1.04
<i>Tomentella</i> sp.1	JQ393144	98	3.31	0.22	0.80	2.17	0.66	-
<i>Tomentella</i> sp.2	KM402923	95	6.86	5.06	13.75	-	-	-
<i>Tomentella</i> sp.3	GQ900537	99	-	-	2.80	0.39	0.50	-
<i>Tomentella</i> sp.4	EU529972	99	0.25	-	-	-	-	0.70
<i>Tomentella</i> sp.5	EF411112	86	10.48	-	-	-	-	-
<i>Tomentella</i> sp.6	EU625851	95	0.37	-	-	-	2.32	-
<i>Tomentella</i> sp.7	KT020809	96	1.16	-	-	-	-	-
<i>Tomentella</i> sp.8	EF218840	98	-	0.86	-	-	-	-
<i>Tomentella</i> sp.9	FR852152	98	-	0.11	-	-	0.30	-
<i>Tomentella</i> sp.10	KT272128	95	-	-	0.74	-	-	-
<i>Tomentella</i> sp.11	AB848667	98	-	-	-	0.17	-	-
<i>Tomentella</i> sp.12	JQ393143	97	-	-	-	0.44	-	-
<i>Tomentella</i> sp.13	HQ271388	92	-	-	-	5.73	-	-
<i>Tomentella</i> sp.14	AB839403	99	-	-	-	-	-	0.75
<i>Tomentella</i> sp.15	GQ219890	93	-	-	-	-	0.36	-
<i>Tomentellopsis</i> sp.1	AJ410756	86	-	-	0.11	-	-	-
<i>Tomentellopsis</i> sp.2	KJ769322	97	0.37	-	-	-	-	-
<i>Tomentellopsis zygodesmoides</i>	KP814159	97	-	-	-	0.33	-	-
<i>Tricholoma</i> sp.	KJ937000	95	1.96	-	-	0.78	-	0.17
<i>Tricholoma saponaceum</i>	DQ370440	99	-	-	-	-	-	9.27
<i>Tuber</i> sp.1	KF744063	88	-	0.54	-	-	-	-
<i>Tuber</i> sp.2	AB553505	99	0.92	-	1.88	5.34	-	-

^aIntensity treatments conducted under the low-thinning method. ^bMethod treatments conducted under moderate thinning intensity.