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Effects of Canopy Cover on Morphological Types of Ectomycorrhizae of Northern Red Oak Seedling^{*} 林冠郁闭度对美国北红橡幼苗外生菌根形态类型的影响

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Abstract Morphological types of ectomycorrhizae (ECM) on northern red oak (Quercus rubra L) seedlings were investigated at four levels of canopy cover in approximately 90-year-old northern red oak forests in intermediate quality sites of northern Lower Michigan. Four levels of canopy cover (clearcut, 25% (50% first year), 75%, and uncut) were created by removing various amounts of overstory trees. Northern red oak seedlings, originated from a common seed source, were established artificially to simulate natural regeneration. The seedlings were sampled to classify and quantify their ECM by morphological type during each of the first two growing seasons. ECM fruiting bodies were also collected, identified and analyzed. Based on ECM morphology, a total of seven ECM morpho-types was recognized on the northern red oak seedlings during the first two growing seasons. More than 94% of the ECM were from four of the seven types. None of the ECM types were identified into definite fungal associates. However, attempt has been made to relate these ECM types to the most likely fungal species or species groups based on references to published descriptions and/or photographies. A greater percentage of type III (shiny white) ECM was found in the closed canopy plots where soil moisture is the lowest among canopy treatments. This incident indicated that type III ECM may tolerate low levels of soil moisture by their abundant extramatrical hyphae and /or rhizomorphs. The percentage of type I (Cenococcum Hike) ECM was greatest in clearcuts, suggesting that it may be resistant to high soil temperatures after canopy removal (soil temperature in clearcut was 5 $^{\circ}$ higher than that in uncut stands). These shift in ECM types reflects the complexity and importance of ECM diversity in response to different levels of canopy cover. From ecological perspective, ECM morphology may be more meaningful than ECM fungal species.

Key words ectomy corrhizae, ECM morpho-type, northern red oak, canopy cover, Quercus rubra

摘要 在密之根州 (美国)南半岛北部地区林龄大约90年的北红橡 (northern red oak, Quercus rubra L.)林中, 调查了北红橡幼苗外生菌根形态类型。实验地的立地质量为中等水平。通过砍伐不同数量的上层林木,形成0% (皆伐)、25% (第一年50%)、75%、100% (高度郁闭) 4种林冠郁闭度。北红橡幼苗是由模仿自然更新人工播 育种出,种源一致。在头2年,将幼苗上的外生菌根分类、描述和计数,同时收集菌根菌子实体进行鉴定和分析。 根据形态特征,将外生菌根分为7个类型,其中4个类型占菌根总数的94%。据现有资料 (已发表的论文及图片 等),把这些菌根类型的共生菌种或菌种组归纳。发现,在林冠高度郁闭并由此降低土壤水分的情况下,类型III 的菌根最多,表明这类菌根具有耐旱性;类型I 的菌根在皆伐区最多,表明其有耐较高土壤温度能力,因为皆 伐后土壤温度比对照林分高出5^C以上、菌根类型随林冠郁闭度变化而变化的现象,反映了菌根关系的复杂性和 多样性。本研究结果表明,探明菌根的形态类型比探明菌根菌的种类更有意义。 关键词 外生菌根 菌根形态类型 北红橡 林冠郁闭度 Quercus rubra 中图法分类号 S 718.81

Numereous studies have conducted on morphological characteristics of ectomycorrhizae (ECM) from different tree species including *Pinus* resinosa^[1], *P. sylvistris*^[2], *Picea abies*^[3], *P. rubens*^[4], and *Quercus acutissima*^[5], and *Q. robur*^[6].

Although these works have provided large amounts of valuable information in understanding mycorrhizal relationships and their characteristics and behaviors, the ECM characteristics in association with various levels of canopy cover have not

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been documented. The understanding of ECM morpho-types in relation to different canopy cover levels may help to maintain mycorrhizal fungi diversity in forest ecosystems. A number of studies have reported change in mycorrhizal populations following forest management practices, such as harvesting, site preparation, and burning¹⁷⁹. Changes in morphological types of ECM of *Pinus resinosa* seedlings have been observed by Richter and Bruhn^[1] for more than three years time period. The author found the ECM types tend to shift from nursary types to late stage type. Wu et al^[10] also reported that a negative correlation exists between brown-type ECM per gram dry root and field age of *P*. resinosa seedlings. Zhou et al^[11]. reported that a complete removal of canopy inhibited overall ECM development of Quercus rubra seedlings, while partial removal of the canopies stimulated such development.

Marx^[12] indicated that difficulty in oak regeneration may be due to the poor development of certain morphological type of ECM or ECM as a whole besides the differences in light conditions. However, ECM development is strongly related to the environmental conditions^[13~14]. Thus, the objectives of this study were to determine recognizable ECM morphological types on norhtern red oak seedlings and their variabilities in association with different levels of canopy cover in oak forests.

1 Methods

1.1 Location of the Study Area

The study area is located in the Graying Subdistrict of the Highplains District of Ecological Region II in northern Lower Michigan (longitude 84° 41' to $84^{\circ}45^{\circ}$ W, latitude $44^{\circ}14'$ to $44^{\circ}31'$ N)^[15]. A greater detailed description is available in Zhou et al^[11].

Two adjacent northern red oak stands in southwest Crawford County (T25N, R4W, Sections 26 and 35) were used as study sites. Limited stand size and previous disturbance precluded the use of a single oak stand. These stands are owned and managed by the Michigan Department of Natural Resources. The stands occur on pitted outwash and fall into Site Unit 5 (Oak-Pine-Vaccinum) of the Ecological Classification of the State Upland Forests in northern Lower Michigan^[16]. Soils were sandy.

Three blocks were identified from these two 90year-old northern red oak stands. Two of the oak blocks were in the more downslope (northern) of the two adjacent oak stands while the third block was in the more upslope (southern) stand. Percent slope averaged 5%, 2%, and 6% for block I, II, and III, respectively.

Each block consisted of four randomly-assigned overstory treatments (66 m× 66 m in size) manipulated to create ‰ canopy cover (clearcut), 2‰ canopy cover (50‰ first year), 75‰ canopy cover, and 100‰ canopy cover (uncut). The actual percent canopy cover varied in each overstory treatment after the manipulation, i.e., 0%, $25\% \sim 29\%$, $(45\% \sim 67\%$ first year), $67\% \sim 77\%$ and $75\% \sim 95\%$ for the four treatments, respectively. Sampling of each overstory treatment plot was confined to the central $30 \text{ m} \times 30 \text{ m}$, with an 18 m wide buffer zone to reduce edge effects.

All treatments were initiated in late summerearly fall of 1990. Varying amounts of canopy were removed by thinning from below. Stems with diameter at breast height (DBH) 2.54 cm or larger were considered as overstory trees. Large logging residues in the experimental plots were removed, by hands or logging machine, beyond the sampling area. A spherical densiometer was used to measure canopy cover in order to obtain comparable overstory treatments^[17].

1. 2 Sampling Scheme

All acorns were from the vicinity of the University of Michigan Biological Station, approximately 125 km north of the experimental sites. Acorns were planted in May 1991, on a 15 cm × 15 cm spacing at three randomly located points representing the intersection of a 2 m \times 2 m grid in each plot. A total of six seedlings was sampled from each subplot during the first growing season and 12 seedlings during the second growing season. One set of samples (two seedling per plot) was randomly collected and evaluated across all treatments before another set of samples was taken. Sampling began in early July the first year and late May the second year, and ended in late September in both years. A soil column (minimum of 12 cm in diameter by 15 cm in depth) containing a seedling was excavated to obtain nearly a complete root system and to prevent root damage and desiccation during transport. The soil columns with seedlings were stored in a walk-in cooler ($3^{\circ}C \sim 5^{\circ}C$) immediately after they were brought back to the laboratory.

Soil moisture at 0 cm^{\sim} 15 cm depth and soil temperature at 0 cm^{\sim} 7.5 cm depth were recorded approximately biweekly^[11].

1. 3 ECM Characterization and Quantification

The root systems were washed gently to remove soil particles and to minimize damage to mycorrhizal root tips. Number of short roots by ECM morpho-type were quantified by examining all root tips under a dissecting microscope ($10 \le -40 \ge$) during the first year, and on three randomly-selected lateral roots (0.5 mm or larger in diameter) of each seedling the second year. Each ECM root tip was counted to account for differences between single and multiple branched ECM. Percent ECM by morpho-type were calculated.

Root tips were sectioned and observed under a compound microscope to confirm the presence or absence of a fungal mantle at $200 \times \sim 400 \times$ magnification, and to observe Hartig-net and hyphal structure at $400 \times \sim 1000 \times$ magnification. The criteria used in this study to separate morpho-types were based mainly on morphological features including color, shape, branching patterns, size and surface texture, and hyphal features including septate, clamp-connection, color and diameter^{$[6, 18^{-}21]}$.</sup>

1. 4 Fruiting Body Survey

All mushrooms (except for those growing on litter, dead wood, or on any living tree) in the experimental area were collected every two to three weeks from late July to the end of September each year, and tallied with respect to canopy cover treatment. This method may be have excluded some ECM fungi which grow on litter or dead woods^[22]. Abundance was estimated for each genus or fungal species. Identification of fruiting bodies was based mainly on references [23~ 26]. Identification of collected specimens was corroborated by Dana L. Richter (Michigan Technological University, USA).

1. 5 Statistical Ananlysis

One-way analyses of variance (ANOV A) algorithms by SAS (Version 6)^[27] were used to determine if percent ECM morpho-types differed among canopy cover treatments. The data were the averages of two years since they showed a very similar pattern across the canopy cover treatments both years. Tukey's test was used for multiple comparisons, which is more conservative than Duncan's or Fisher's Least Significant Difference procedure^[28]. Unless indicated otherwise, $\alpha = 0.05$ level.

2 **Results and Discussion**

2.1 ECM Morpho-Types

A total of seven morpho-types of ectomycorrhizae were classified from northern red oak seedlings under two years of age based on field observations with the aid of dissecting and compound microscopes. Detailed descriptions of each type are given in Table 1. Types I, II, III and IV were the major ECM morpho-types encountered, and accounting for 94% of the total ECM short roots, while the sum of types V, VI and VII did not exceed six percent.

Although the color of hyphae and mycorrhizal mantle is frequently stable^[19], it may change at different developmental stages^[4, 29, 30] and substrate p H value^[20,31]. Oh et al^[5] classified ECM from Quercus acutissima seedlings into seven types in order to determine which ECM types provide a greater effect upon the seedling dry mass. Newton^[6] separated ECM of *Q. robur* L. into a number of types based on gross morphological characteristics and microscopic characteristics in an attempt to determine factors which influence the variation in the extent of colonization of mycorrhizal types (or fungal species) in a forested sites and the consequences for seedling growth. Majumdar et $al^{[32]}$ classified mycorrhizae of Q. rubra and Q. alba into two types pinnate and beaded types. Therefore, it is clear, based on the above reviews, that the criteria and techniques used by different researchers to sepa rate ECM into morpho-types make them difficult to compare and to link to definite fungal associates.

In my study, criteria for separation of morphotypes were similar to those of Newton^[6], except that mantle structure was not described. The linkage between the morpho-types and fungal associates cannot

 Table 1
 Macro-and micro- characteristics of ectomycorrhizal (ECM) morphological types on nothern red oak seedlings (under

 2 years of age) in northern Lower Michigan

Type	Characteristics
ECM Type ^I (black)	Mycorthizae are short and often club-shaped. They are single, but may occasionally produce on eor more branches. The mycor- hizal tip is 0.24 mm ^{\sim} 0.34 mm in diameter and 0.44 mm ^{\sim} 1.00 mm in length. The mycorrhizae are black in apparence. Coarse, black hyphae are frequently observed radiating from the mantle surface. The hyphal diameter is 4.0 ^{μ} 5.5 ^{μ} . No clamp connec- tions were observed. The mantle is 25 ^{μ} \sim 38 ^{μ} in thick ness and Hartig-net 6 ^{μ} \sim 10 ^{μ} in depth.
ECM TypeII (dull white)	My corrhizae are usually single with a very smooth surface. The my corrhizal tip is 0. 20 mm \sim 0. 35 mm in diameter and 1. 20 mm \sim 2 50 mm in length. The my corrhizae are dull white or slightly brownish white. The hyphae are $3\mu \sim 4\mu$ in diameter and hya- line. Clamp connections were occasionally observed, suggesting a member of Basidiomycetes. The mantle is $21\mu \sim 45\mu$ in thick- ness and Hartig-net $24\mu \sim 28\mu$ in depth.
ECM TypeIII (shiny white)	My corthizae are usually irregularly pinnate, dichotomous-like. The my corrhizal tip is 0.2 mm ⁻ 0.3 mm in diameter and 1.1 mm \sim 1.2 mm in length. The my corthizae are shiny, silvery white. The hyphae is 2.0 μ 2.5 μ diameter and hyaline. No clamp connections were observed. The usually produce abundant interconnected filaments and thizomorphs around the short roots. The mantle is 30 μ 45 μ in thickess and Hartig-net 6 μ 8 μ in depth.
ECM TypeIV (brown)	My corrhizae are usually single, but sometimes they are dichotomous. The my corrhizal tip is 0.3 mm ^{\sim} 0.5 mm in diameter and 1.0 mm ^{\sim} 3.2 mm in length. The my corrhizae are brown or dark brown in color. The hyphae are usually dark with highly-frequent clamp connections. The hyphae are $3^{\mu} \sim 4^{\mu}$ in diameter. The mantle is $24^{\mu} \sim 30^{\mu}$ in thick ness and Hartig-net $42^{\mu} \sim 48^{\mu}$ in depth.
ECM TypeV (dark brown)	My corrhizae are usually monopodial-pinnate, but som etimes may be single. The my corrhizal tip is 0. 20 mm ⁻ 0. 25 mm in diameter and 0. 80 mm ⁻ 1. 00 mm in length. The my corrhizae are dark brown or nearly black, with shiny patches often observed on the mantle surface. The hyphae are thick and somewhat woolly. Clamp connections were rarely observed. The mantle is $36\mu \sim 42\mu$ in thick ness and Hartig-net $50\mu \sim 53\mu$ in depth.
ECM Type VI (yellow)	Mycorthizae are usually singles but sometime may produce one or two branches. The mycorthizae are bright yellow. The bright yellow rhizomorphs growing off in flat angles are usually present.
ECM Type VII (blue)	My corrhizae are usually coralloid, but sometime may appear as single tips. The my corrhizal tip is 0. 25 mm ⁻ 0. 30 mm in diameter and 0. 80 mm ⁻ 2. 20 mm in length. The my corrhizae are blue or purplish blue with cottony blue hyphae, and somewhat shiny sur-

blue) and 0.80 mm⁻² 2.20 mm in length. The mycorthizae are blue or purplish blue with cottony blue hyphae, and somewhat shiny surface. The hyphae are highly variable in diameter manging from 2^{μ} to 5^{μ} . Clamp connections are occasionally observed. The smaller hyphae often fuse together and were frequently septate. The mantle is very losse and approximately $18\mu^{-2}$ 26μ in thickness and the Hartig-net is poorly developed. The variable cottony hyphae could have been a mixture of two or more fungi. be achieved with certainty, but some degree of generalization may be applied. Cenococcum geophilum (sensu lato) mycorrhizae have consistent features on a wide range of hosts such as Fagus^[33], Picea^[2,4,31], Pinus^[1,34] and Tilia^[30], which show a stable black mantle and coarse hyphae radiating outward from the surface. Cenococcum -like ECM on northern red oak seedlings were described in this study as type I (black) (Table 1). Table 2 indicates that Cenococcum is a known fungal associate of northern red oak^[35,37]. The type II (dull white) ECM resembles the morpho-types of Amanita muscaria on Picea abies and Pinus sylvestris, or Inocybe petiginosa on Picea sitchensis^[34], or Scleroderma spp. on Pinus resinosa^[22]. Neither

Table 2 Mycorrhizal fungal associates of northern red oak (Quercus rubra L) reported elsewhere, data from various sources

Fungus associate	Reference	notes
Boletus bicolor var. bicolor	[39]	Fruit body survey
B. griseus	[39]	Fruit body survey
B. russellii	[39]	Fruit body survey
Boletellus chrysenteroides	[39]	Fruit body survey
Cenococcum geophilum	[36]	
	[37]	Inoculation
Clitocybe candicans	[Trappe 1962, Ph. D thesis], [35] ¹	Unknown
Cortinarius rubrip es	[Kauffman 1906], [35] ¹	Unknown
Hebeloma crustul in i forme	[40]	Inoculation
<i>H</i> . sp.	[41]	Fruit body survey
Inocybe sp.	[41]	Fruit body survey
Laccaria bi col or	[42]	Inoculation
L. laccata ²	[41]	Fruit body survey
Lactarius argillaæifolius	[43]	Fruit body survey
L. cam phoratus	[43]	Fruit body survey
L. chrysorheus	[43]	Fruit body survey
L. gerar di i	[43]	Fruit body survey
L. louisii	[43]	Fruit body survey
L. peckii	[43]	Fruit body survey
L. pseudo f lexuosus	[43]	Fruit body survey
L. pyrog alus	[43]	Fruit body survey
L. vol emus	[43]	Fruit body survey
Leccinum rugosiceps	[39]	Fruit body survey
P isol i thus t inctor ius	[44, 45]	
	[40]	Inoculation
<i>Rh izo pogon</i> sp.	[Imshemetshii 1967]	
	[49] ¹	Unknown
Russula emetica	[Pennington 1908], [35] ¹	Unknown
Scleroderma areolatum	[46]	Fruit body survey
S. auranteum	[36]	
	[44]	Inoculation
S. cep a	[46]	Fruit body survey
S. citrinum	[46]	Fruit body survey
S. meridionale	[46]	Fruit body survey
S. polyrh iz um	[46]	Fruit body survey
Sph aerosporel la brunnea	[47]	Inoculation
Strobilom yæs f loccopus	[39]	Fruit body survey
Suillus luteus	[48, 49]	Inoculation
Th elephora terrestris	[Imshemetshii 1967],	
	[49] ¹	U nknow n
Tylopilus rubrobrunneus	[39]	Fruit body survey

1 These references were cited in either references [35] or [49]; 2 This fungus did not colonized *Q. rubra* in the greenhouse (Reber 1991).

Table 3Abundance of fruiting bodies of putative ectomycor-rhizal fungi observed from August to October, 1991 and 1992in northern red oak stands in northern Lower Michigan

Name	Oak Stand	Name	Oak Stand
Amanita brunnescens	+ + + +	L. spp.	+
A.citrina	+	Lactarius piperatus	+ +
A. muscaria v. formos a	+	L. spp.	+ + +
A. rubescens	+ +	Russula brevipes	+
A. sp.	+	R. krombholzii	+
A.virosa	+ + +	R. spp (red)	+ + + +
Cantharellus ignicolor	+ +	R. var iz tz	+ + + +
Dentinum rep andum	+ + +	Tricholoma spp.	+ +
<i>Hygrophorus</i> spp.	+	To tal Taxa	18
Laccaria laccata	+ + +		

+ Present, 1~3 individuals in total; + + Common, 4~6 individuals in total; + + + Abundant, 7~15 individuals in total; + + + + Very abundant, more than 16 individuals in total.

Amanita muscaria nor Inocybe petiginosa have been reported to be fungal associates of northern red oak, although some members of these two genera may associate with other oak species^[38]. In this study, Amanita spp. fruiting bodies were observed in the northern red oak stands (Table 3).

The type III ECM (shiny white) resembles the morpho-types of *Leccinum* sp., *Lactarius* sp., *Tricholoma* spp. and *Cortinarius* spp. on one or more of following genera, *Betula*, *Quercus*, *Piœa*, and *Pinus*^[1,34]. Among these fungi, *Cortinarius rubripes*, *Leccinum rugosiceps* and *Lactarius* spp. have been reported to be fungal associate of northern red oak (Table 2), although all of them may associate with other oak species^[38]. In this study, fruiting bodies of *Lactarius* spp. and *Tricholoma* spp. were found in the northern red oak stands (Table 3).

The type VI (yellow) ECM resembles the ECM of *Piloderma croceum* on *Picea* species described by Mikola^[31]. However, the latter was not found on deciduous trees in central Finland^[31]. The other ECM types listed in Table 1 cannot be linked to possible mycorrhizal fungal species based on my field observation alone. More data on mantle, Hartig net and fungal structures are needed to link them to more definite fungal associates.

Previous studies have indicated that differences in the type of ramification, shape dimmensions, shape and orientation of cortical cells and depth of Hartig-net exist on different host species with the same fungal isolate [50]. According to the authors, the morphology and anatomy of mycorrhizae vary among developmental stages, more specifically, with respect to length, diameter, color, occurence of intracellular hyphae, and deposition of phenolic substances. Oh et al^[5] indicated that *Pisolithus tinctorius* can form coralloid type or linear type ECM on the same oak species. $Marx^{[51]}$ reported that *P*. tinctorius can form simple, coralloid or multiple coralloid types on Pinus taeda. Cenococcum geophilum can form several different morphological features on Tilia americana^[30] and Picea rubens^[4], depending on its developmental stage. This ECM type, which is white during the early stages of development, turns brown in the mature stage and

 Table 4
 Percent morphological type of ectomycorrhizae (ECM) on northern red oak seedlings and total number of fruiting bodies (FB) of potential ECM fungi during the first two growing seasons after canopy manipulations of oak stands

Canopy cover	Percent morphological type of ECM (%)						$FB(no)^{**}$	
(%)	TypeI	TypeII	TypeIII	TypeIV	TypeV	Ty pe VI	Type VII	1 D (10.)
0 (Clearcut)	35. 3a*	16. 4a	7. 7b	38. 9a	1. 9ab	0. Ob	0. 0b	0
25	17. 5b	17. 9 _a	14. 3ab	47. 0 _a	3. 1 _a	0. 1 _{ab}	0.4ab	51
75	19. 8b	13. 6a	12. 0ab	48. 3a	4. 9a	0. 2ab	1. 4a	62
100 (Uncut)	23. 3 _{ab}	17. 5 _a	17. 6 _a	38. 5 _a	0. 8b	0. 7 _a	0. 5 _a b	47

* The same letter shared by canopy levels indicates no significant differences at the 5% level; * * The data are not enough to analyze statistically.

black in the senescent stage. This ECM type could also be a species complex or different taxa^[52]. In addition, Majumdar et al^[32] indicated that beaded mycorrhizae on Q. *rubra* and Q. *alba* were associated with highly acidic stress soils.

Based on the above findings, it may be concluded that ECM morpho-types are not only host and /or developmental-stage dependent, but also reflect environmental conditions. It is a problem, therefore, to link ECM morpho-types to specific ECM fungi without complete hyphal structure, comparison of isolates from fruit bodies and mycorrhizae, and genetic information. From an ecological view point, it is important to have designated ECM morpho-types of a host to reflect mycorrhizal conditions within a defined environment. However, caution must be exercized to generalize in a broader way that a specific fungal species related to a certain ECM morphotype. Nevertheless, when an accurate fungal species of a mycorrhizal root tip is needed, DNA sequence analysis will offer considerable promise in this regard (R. Fogel, University of Michigan, personal communication).

2. 2 Percentage of ECM Morpho-Type

Table 4 shows ECM morpho-types in response to the canopy cover treatments. The type I (black) ECM was significantly greater in the clearcut than in the 75% canopy cover treatment. ECM Type V II showed greater colonization rates in the intermediate canopy cover treatments.

The more abundant type I (*Cenococcum* -like) ECM in clearcuts than in other canopy cover treatments has been reported elsewhere to tolerate drought conditions^[53-55]. However, in my study soil moisture levels and soil temperature in the clearcut treatment were the greatest among the canopy cover treatments^[11]. Therefore, in northern Lower Michigan, a tolerance of *Cenococcum* -like ECM to high soil temperatures may be more important in establishment of northern red oak seedlings than tolerance to reduced moisture.

In contrast, the increase in percentage of type III ECM with increasing canopy cover may be related to its tolerance of low soil moisture levels since soil moisture was declining with increasing canopy cover. Although type III ECM may be formed by various fungi, as discussed earlier, they all exhibit abundant extramatrical hyphae and rhizomorphs with which to extract more water from lower soil profiles and surrounding organic materials. It seems likely that the same ECM morpho-type formed by different fungal species would have similar ecological functions in forest ecosystems under investigation here. These morpho-types have ecological significance because of certain common attributes that relate to their ability to tolerate certain environmental conditions and/or sequester resources.

The type VI (*Piloderma* -like) ECM was not observed in the clearcut treatments in either year and tended to increase in number with increasing canopy cover (Table 4). This finding supports the result of Mikola^[31] on *Picea*. This ECM type produces a large mycelial network in the soil humus (personal observation), suggesting that a small number of ECM short roots in this particular case may be important to ecosystem structure and function^[50].

Some ECM morpho-types were apparently inhibited by varying degrees of canopy removal, while others were stimulated. These results suggest that the composition of ECM types can be modified by overstory manipulations. Shifts in ECM type abundance in response to changes in environmental factors associated with disturbance have been reported elsewhere^[11,57-59]. Such shift of ECM types may be important in maintaining mycorrhizal fungi diversity, thereby contributing to the "buffering capacity" of the forest ecosystem^[60]. More specifically, different ECM fungi may benefit the host plants in different ways, e. g., some increase water and nutrient uptake, others resist to environmental stresses at certain times during plant development.

2. 3 ECM Fungal Sporocarps

A total of 8 genera of potential ECM fungal fruiting bodies were collected in the experimental plots over two growing seasons (Table 3). No fruiting bodies were observed in clearcuts and there was slightly more sporocarp production in the 75% canopy cover treatments than in the lower and higher canopy cover treatments (Table 4).

Fruiting bodies of *Laccaria*, *Lactarius*, and Russula found in my study (Table 3) corroborated previous reports that they are fungal associates of northern red oak (Table 2). Amanita, Cantharellus, and Tricholoma are not known to associate with northern red oak, but have been reported to associate with other oak species^[38]. The other Dentim um fungal sporocarps, i.e., and Hygrophorus, collected from my study sites (Table 3) may or may not be mycorrhizal fungi and /or mycorrhizal fungi associated with northern red oak.

The absence of ECM fruiting bodies in the clearcut treatments supports that many ECM fungi never fruit soon after clearcutting in areas where they were previously found^[1,61]. This effect may be explained by a lack of food for sporocarp production by ECM fungi^[62].

3 Conclusions

My data indicated that even if the fungal associates are different, their common morphology, such as abundant extramatrical hyphae and rhizomorphs, may have similar ecological functions in the forest ecosystems. The canopy cover treatments have modified ECM-type composition on northern red oak seedlings. This modification may suggest that ecological specific be more important than host preference in mycorrhizal associations. Such shifts in ECM types also reflect the complexity and importance of mycorrhizal diversity in response to canopy cover levels.

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References

- Richter D L, Bruhn J N. Mycorrhizal fungus colonization of *Pinus resinosa* Ait. transplanted on northern hardwood clearcuts. Soil Biol Biochem, 1993, 25 355~ 369.
- 2 Agerer R. Colour atlas of ectomycorrhizae. Einhorn-Verlag Eduard Dietenberger. 1987.
- 3 Huag I, Pritsch K. Ectomycorrhizal types of spruce (*Picea abies* (L.) Karst.) in the Black Forest a microscopical atlas. Kernforschungszentrum Karksruhe. 1992, 89.
- Glenn M G, Wagner W S, Webb S L. Mycorrhizal status of mature red spruce (*Picea rubens*) in mesic and wetland sites of northwestern New Jersey. Can J For Res, 1991, 21: 741~749.
- 5 Oh K I, Jung N C, Park W S. Studies of growth response and ectomy corrhizal identification of *Quercus acutissima* seedling inoculated with ectomy corrhizal fungi isolated in Chonnam Province. J Korean For Soc, 1993, 82 366~ 380.
- 6 Newton A C. Mineral nutrition and mycorrhizal infection of seedling oak and birch III Epidemiological aspects of ectomycorrhizal infection, and the relationship to seedling growth. New Phytol, 1991, 117 53~ 60.
- 7 Amaranthus M P, Perry D A. Effect of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, non-reforested clear-cuts. Can J For Res, 1987, 17 944~ 950.
- 8 Harvey A E, Jurgensen M F, Larsen M J. Clear-cut harvesting and ectomycorrhizae survival of activity on residual roots and influence on a bordering forest stand in western Montana. Can J For Res, 1980. 10 300 303.
- 9 Perry D A, Molina R, Amaranthus M P. Mycorrhizae,

mycorrhizospheres, and reforestation current knowledge and research needs. Can J For Res, 1987. 17: 929~ 940.

- 10 Wu Y, Gale M R, Cattelino P Jet al.. Temporal dynamics of ectomycorrhizal populations and seedling characteristics on red pine (*Pinus resinosa*). Can J For Res, 1993, 23: 810- 815.
- 11 Zhou M, Sharik T L, Jurgensen M F et al.. Ectomycorrhizal colonization of *Quercus rubra* seedlings in response to vegetation removals in oak and pine stands. For Ecol Mange, 1997, 93 91~99.
- 12 Marx D H. Synthesis of ectomycorrhizae by different fungion northern red oak seedlings. USDA Forest Service, Research Note, 1979. SE- 282. 8.
- 13 Amaranthus M P. Mycorrhizas, forest disturbance and regeneration in the Pacific northern United States. In Read D J, Lewis D H, Fitter A H, et al. Mycorrhizas in Ecosystems. C A B International, Wallingford, UK, 1992. 202- 207.
- 14 Zhou M, Sharik T L. Ectomycorrhizal associations of northern red oak (*Quercus rubra*) seedlings along an environmental gradient. Can J For Res, 1997, 27 1705~ 1713.
- 15 Albert D A, Denton S R, Barnes B V. Regional landscape ecosystems of Michigan. School of Natural Resources, University of Michigan, 1986.
- 16 Pregitzer C, Host G E, Greaney P J An ecological classification of the state upland forests in northern Lower Michigan. Version 1. 1. Forest Ecology Laboratory, Department of Forestry, Michigan State University, East Lansing, Michigan. 1987.
- 17 Lemmon P E. A spherical densiometer for estimating forest overstory density. For Sci, 1956, 2 314-230.
- 18 Melville L H, Massicotte H B, Peterson R L. Morphological variations in developing ectomycorrhizae of *Dryas integrifolia* and five fungal species. Scanning Microscopy, 1987, 1: 1455~ 1464.
- 19 Trappe J M. Principles of classifying ectotrophic mycorrhize for identification of fungal symbionts. International Union Forest Research Organizations. 14th Kongress Proceedings, 1967, set 24, 46~ 59.
- 20 Wilcox H E. Morphology and development of ecto-and ectendomycorrhizae. 1982, 103-113. In: Schenck N C. Methods and Principles of Mycorrhizal Research. The American Phytopathological Society, St. Paul, Minnesota.
- 21 Zak B Classification of ectomycorrhizae. In Marks G C, Kozlowski T T. Ectomycorrhizae-Their Ecology and Physiology. New York Academic Press, 1973. 43-78.
- 22 Richter D L, Bruhn J N. *Pinus resinosa* ectomy corrhizae seven host-fungus combinations synthesized in pure culture. Symbiosis, 1989, 7 211- 228.
- 23 Lincoff G H, Nehring C. The Audubon Society field guide to North American mushrooms. Alfred A. Knopf, New York. 1989, 926.
- 24 Pacioni G, Lincoff G. Simon& Schuster s guide to mushrooms. Simon& Schuster Inc. New York. 1981. 511.
- 25 Smith A H, Smith H V, Weber N S. How to know the gilled mushrooms. W. C. Brown Co, Dubuque, Iowa, 1979. 334.
- 26 Smith HV, Smith A H. How to know the non-gilled fleshy fungi. W. C. Brown Co, Dubuque, Iowa, 1973, 401.
- 27 SAS Institute Inc. SAS/STAT User's guide. Version 6, 4th ed. Volume 2, Cary, NC. 1989.
- 28 Ott L. A introduction to statistical methods and data analysis. Boston Duxbury Press, 1984. 775.
- 29 Jacobs P F, Peterson R L, Massicotte H B. Altered fun-

gal morphogenesis during early stages of ectomycorrhiza formation in *Eucalyptus pilularis*. Scanning Microscopy, 1989, 3 249~ 255.

- 30 Park J Y. A change in color of aging mycorrhizal roots of *Tilia americana* formed by *Cenococcum graniforme*. Can J Bot, 1970, 48 1339~ 1341.
- 31 Mikola P. The bright yellow mycorrhiza of Raw Humus [Comptes rendus]. International Union of Forestry Research Organizations. 13th Kongress Verhandlungen. Proceedings, 1962. 4~ 24.
- 32 Majumdar S K, Derivaux C C, Hofkin S L et al. Morphological studies of oak mycorrhizae from two forest habitats differing in their sensitivities to acid precipitation in eastern pennsylvania. Phytomorphology, 1992, 42 109~ 115.
- 33 Hollett B P, Jackson M T. Quantitative aspects of the association of *Cenococcum graniforme* with *Fagus* grandifolia in Indiana. For Sci, 1976, 22: 127-130.
- 34 Ingleby K, Mason P A, Last F T et al. Identification of ectomycorrhizas. Institute of Terrestrial Ecology, Natural Environment Research Council. London HM-SO, 1990, 112.
- 35 Trappe J M. Fungus associates of ectotrophic mycorrhizae. Bot Rev, 1962, 28 538-606
- 36 Beckjord P R, McIntosh M S. Growth and fungal persistence by *Quercus rubra* inoculated with ectomycorrhizal fungi and planted on a clear-cutting and strip mine. Can J Bot, 1984, 62 1571- 1574.
- 37 Timbal J. Gelpe J. Gaybaye J. Preliminary study of the depressive effect of *Molinacaerulea* L. moench on early growth and mycorrhizal status of *Quercusrubra* seedlings. Ann Sci For, (Paris), 1990, 47 643- 649.
- 38 Zhou M. Relationship of northern red oak (*Quercus rubra* L.) seedlings to ectomy corrhizae in response to overstory and understory manipulations in oak and pine stands [Ph. D. dissertation]. Michigan Technological University, Houghton. 1994, 192.
- 39 Homola R L, Mistretta P A. Ectomycorrhizae of Maine a listing of Boletaceae with the associated hosts. Life Sciences and Agriculture Experiment Station, University of Maine at Orono, Orono, Maine 04469, Bulletin, 1977, 735 21.
- 40 Reber R T. Quercus rubra L. and ectomycorrhizae natural colonization in field plantings and fertilization effects on specific fungal species and growth parameters in a greenhouse study [M S Thesis]. Purdue University, 1991, 100.
- 41 Dixon R K. Nursery inoculation of northern red oak seed-

lings with the fungal symbiont *Suillus luteus*. In 4th workshop on seedling physiology and growth problems in oak plantings. USDA Forest Service, North Central Forest Experiment Station, General Technical Report NC-139. 1989, 14.

- 42 Gagnon J, Langlois C G, Gaybaye J. Growth and ectomycorrhiza formation of container-grown red oak seedlings as a function of nitrogen fertilization and inoculum type of *Laccaria-bicolor*. Can J For Res, 1991, 21 966-973.
- Homola R L, Czapowskyj M M. Ectomycorrhizae of Maine 2 a listing of *Lactarius* with the associated hosts (with additional information on edibility). Life Sciences and Agriculture Experiment Station, University of Maine at Orono, Orono, Maine 04469. Bulletin, 1981, 779 19.
- 44 Beckjord P R, Melhuish J H Jr, McIntosh M S. Effects of nitrogen and phosphorus fertilization on growth and

formation of ectomycorrhizae of *Quercus alba* and *Q. rubra* seedlings by *Pisolithus tinctorius* and *Scleroderma auranteum*. Can J Bot, 1985, 63 1677-1680.

- 45 Pope P E. Pisolithus tinctorius increases the size of nursery grown red oak seedlings. New Forests, 1988, 2 5~ 16.
- 46 Richter D L. Six species of Scleroderma (Gasteromycetes, Sclerodermatales) described from pure cultures. Mycotaxon, 1992, 45 461~471.
- 47 Meotto F, Carraturo P. Ectomycorrhizae of Sphaerosporella brunnea on plants inoculated with Tuber magnatum. Allionia, 1988, 28 109~ 116.
- 48 Dixon R K. Response of ectomycorrhizal Quercus rubra to soil cadmium, nickel and lead. Soil Bio Biochem, 1988, 20 555- 559.
- 49 Dixon R K, Johnson P S. Synthesis of ectomycorrhizae on northern red oak seedlings in a Michigan nursery. J Arboricult, 1992, 18 266-272.
- 50 Pillukat A, Agerer R. Studies on ectomycorrhizas XI: comparative investigations on the tree-dependent vanability of the ectomycorrhizas of *Russula ochroleuca*. Zeitschrift fur Mycologie, 1992, 58 211-242.
- 51 Marx D H. Soil pH and nitrogen influence *Pisolithus* ectomycorrhizal development and growth of Loblolly pine seedlings. For Sci, 1990, 36 224~ 245.
- 52 LoBuglio K F, Rogers S O, Wang C J K. Variation in ibosomal DN A among isolates of the mycorrhizal fungus *Cenococcum geophilum*. Can J Bot, 1991, 69 2331~ 2343.
- 53 Harley J L, Smith S E. Mycorrhizal symbiosis. London Academic Press, 1983. 483.
- 54 Read D J, Boyd R. Water relations of mycorrhizal fungi and their host plants. In Ayres P G, Boddy L. Water, Fungi and Plants. British Mycological Society, 1986. 287
 ~ 303, 413.
- 55 Trappe J M. Selection of fungi for ectomycorrhizal inoculation in nurseries. Ann Res Phytopathol, 1977, 15 203 ~ 222.
- 56 Harvey A E, Jurgensen M F, Larsen M Jetal.. Distribution of active ectomycorrhizal short roots in forest soils of the inland Northwest effects of site and disturbance. USDA Forest Service, Intermountain Research Station, Research paper INT-374, Dec, 1986, 8.
- 57 Borchers S L, Perry D A. Growth and ectomycorrhiza formation of Douglas-fir seedlings grown in soils collected at different distances from pioneering hardwoods in southwest Oregon clear-cuts. Can J For Res, 1990, 20 712-721.
- 58 Pilz D P, Perry D A. Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. Can J For Res, 1984, 14: 94~ 100
- 59 Schoenberger M M, Perry D A. The effect of soil disturbance on growth and ectomycorrhizae of Douglas-fir and western hemlock seedlings a greenhouse bioassay. Can J For Res, 1982, 12 343~ 353.
- 60 Malajczuk N, Reddell P, Brundrett M. Role of ectomycorrhizal fungi in minesite reclamation. In: Pfleger F L, Linderman R G. Mycorrhizae and Plant Health, 1994. 83~ 100.
- 61 Mikola P. Application of mycorrhizal symbiosis in forestry practice. In Marks G C, Kozlowski T T. Ectomycorrhizae-Their Ecology and Physiology. New York Acad Press, 1973. 383~ 411.
- 62 Bjorkman E. Forest tree mycorrhiza-the conditions for its formation and the significance for tree growth and afforestation. Plant and Soil, 1970, 32 589- 610.

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