SYNTHESIS OF ECTOMYCORRHIZAE ON NORTHERN RED OAK SEEDLINGS IN A MICHIGAN NURSERY

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Abstract. Vegetative inoculum of the ectomycorrhizal fungus *Suillus luteus* was thoroughly mixed into fumigated nursery soil, and northern red oak seedlings of four families were evaluated one and two years after sowing for ectomycorrhizal development, growth, and nutrition. At the end of year 1, treated seedlings were successfully inoculated with *S. luteus,* but the percentage varied significantly with family. *Suillus luteus* persisted on lateral roots two years following sowing. Two of four seedling families inoculated with S. *luteus* were significantly larger in size than control plants. These results suggest that the fungal symbiont *S. luteus* can be successfully introduced into nurseries and that early ectomycorrhizal development improves the growth of northern red oak seedlings.

Juvenile growth of bare-root and container-grown oak (*Quercus*) seedlings outplanted in the northern USA is generally unacceptable and is characterized by periodic shoot dieback (16,17,27). Planted oak seedlings that exhibit slow early growth suffer from inadequate root system development and often lack mycorrhizal associations common to naturally occurring seedlings (9,15,17). Ectomycorrhizae provide numerous benefits to host plants, including improved nutrition and growth (5,15,19,28), enhanced drought resistance (8,12) and protection against soil-borne pathogens and toxins (15,28,30).

The root:shoot balance and early growth of oak seedlings after outplanting has been improved by inoculating root systems with selected ectomycorrhizal fungi (5,6,10,11,13). Black oak seedling inoculated with the ectomycorrhizal fungus *Pisolithus tinctorius* have increased root absorptive surface area (8,12). In field trials in the Missouri Ozark region, inoculation with *P. tinctorius* improved the root and shoot growth of newly planted container- and nursery-grown seedlings (10,17). However, *P. tinctorius* is a fungal symbiont that is not well adapted to the climate or soils of the northern USA (22,23,25).

Vegetative inoculum of ectomycorrhizal fungi has been introduced successfully in conifer nurseries worldwide (22,23). However, fungal symbionts and tree hosts often have specific ecological requirements (23,30). Oak ectomycorrhizal associations and their pattern of development differ greatly from those of conifers (9,18,25,26). To realize the benefits of ectomycorrhizal relationships in hardwood nurseries, cultural practices must be developed or adjusted to promote ectomycorrhizal symbiosis (20,21,28). The identification and evaluation of fungal symbionts compatible with oak species under a range of soil and climate factors also must be considered (17).

Oak species form ectomycorrhizal relationships with a number of fungal symbionts (13,26). Ectomycorrhizal colonization of oak by selected fungal symbionts also varies significantly with acorn source (20). Ectomycorrhizal fungi in the genus *Suillus* are compatible with oak species and stimulate early increases in seedling growth (13,15). Some *Suillus* species, however, are not able to withstand the mechanical manipulation required during inoculum preparation and distribution in nurseries (13,30).

The objectives of this study were to: 1) introduce *Suillus luteus*, a confirmed ectomycorrhizal symbiont of several oak species, into fumigated soil in a nursery; and 2) determine the effects of inoculation on the growth, ectomycorrhizal development, and nutrition of four families of northern

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red oak seedlings.

Materials and Methods

Four northern red oak families were collected from four superior phenotypes in Michigan, two each from the Huron-Manistee National Forest, Cadillac Ranger District (families 1 and 2), and the Hiawatha National Forest, Munsing Ranger District (families 3 and 4). Acorns from all four families were sorted by flotation in water and stored at 4°C until sowing (3,4). Vegetative inoculum of *S. luteus* was grown in a vermiculite-peat moss-nutrient mixture for 3 months using techniques described by Marx and Bryan (19). Prior to seedling inoculation, the vegetative mycelium was thoroughly rinsed with deionized water to remove unused nutrients and fungal by-products.

The seedlings were grown at the USDA Forest Service J.W. Toumey Nursery, Watersmeet, Michigan, for 2 years. Nursery beds were tilled and fumigated under polyethylene with 400 kg/ha of methyl bromide (MC-33) before acorn sowing (22,23). Soil chemical properties before the experiment were similar in all beds: pH 5.5 and 272 and 540 µg/g of available P_2O_5 and K_2O, respectively. Dolomitic limestone was added to the beds to raise the exchangeable calcium and magnesium levels to approximately 1.0 meq per 100 g soil. The soil texture was a sandy loam, and organic matter was approximately 2% in all plots.

The study consisted of four replication of a split-plot design with two whole plots and four subplots. For each replication, one plot was inoculated with vegetative inoculum of *S. luteus*, and the remaining plot was an uninoculated control. In the inoculated plots, the vegetative mycelium-vermiculite-peat moss mixture was broadcast evenly over the nursery beds at a concentration of 3.0 L/m^2 of soil surface and was immediately mixed into the upper 20 cm of soil (23). The control plots received an equal amount of autoclaved inoculum applied in the same manner. In all plots, acorns from the four families were row planted in early May to obtain for each family approximately 100 seedlings/m^2 in all subplots.

The nursery beds were fertilized with three applications per year of ammonium sulfate (21-0-0 plus 24% sulphur). The granular fertilizer was applied at a rate of 9.2 kg/ha as a top dressing. The beds were irrigated with tap water as needed. Seedlings in all treatments were horizontally root pruned to a depth of approximately 23 cm in early August of each growing season.

Twenty-five seedlings from randomly selected plots were harvested in September of the first growing season. Seedling root morphology, ectomycorrhizal development, and the presence of fungal fruiting bodies were evaluated (11,23). In September of the second year, all nursery plots were undercut with a root pruning bar at a depth of 36 cm and the seedlings were carefully lifted by hand. Fifty seedlings from each plot were chosen randomly for measurement of dry weight of roots and shoots, shoot length, leaf surface area, and number of primary laterals. Leaf surface area of each seedling sample was determined with a LI-COR LI3000 portable area meter, and shoot and root weight were determined after oven drying (80°C, 48 h). Seedling leaf phosphorus and nitrogen content were analyzed using methods described by Mitchell et al. (24).

Each seedling root system was examined visually for ectomycorrhizae development by the test fungus using techniques described by Dixon et al. (13). To further verify ectomycorrhizae development, approximately 10% of the suspected ectomycorrhizal short roots were sectioned, mounted and examined at 100X for fungus mantle and Hartig net development. Reisolation of test fungi from ectomycorrhizae was attempted after seedling harvest using techniques described by Dixon et al. (11,13). Taxonomic characteristics of the original isolate and reisolates were compared.

Analyses of variance and Duncan's Multiple Range tests were conducted to determine statistically significant effects of inoculation on family seedling growth, ectomycorrhizae development, and nutrition.

Results

Suillus luteus was introduced successfully into nursery beds of northern red oak seedlings (Table 1). However, seedling root systems from the four families exhibited significantly different amounts of ectomycorrhizal colonization in the first year ($P \leq 0.05$). Less than half of the seedlings in family 3 were colonized by *S. luteus*. In contrast, 100% of the inoculated seedlings in families 1 and 2, and 76% in family 4, were colonized with *S. luteus*. Seedlings in the control plots developed little or no *S. luteus* ectomycorrhizae.

Seedlings in the non-inoculated plots developed ectomycorrhizae late in the first growing season and in the second year. Fruiting bodies of *Hebeloma* and *Inocybe* species, *Lacaria laccata*, *S. luteus*, and *Thelephora terrestris* were observed in the control plots in year 2. *Cenococcum geophilum* and *T. terrestris* were the dominant ectomycorrhizal associates of northern red oak in the control plots.

The percentage of *S. luteus* ectomycorrhizal lateral roots per seedling varied with family in year 1 (Table 1). Over 80% of the seedling lateral roots in families 1 and 2 were colonized by *S. luteus*. Seedlings in family 3 developed significantly fewer *S. luteus* ectomycorrhizal primary lateral roots than those in other families. Moreover, the total percentage of ectomycorrhizal lateral roots was significantly lower in family 3 than in the other families ($P \leq 0.05$). The quantity and pattern of seedling colonization by S. *luteus* were not correlated with the number of primary lateral roots per seedling.

Table 1. Ectomycorrhizae development of seedlings inoculated with *S. luteus* after one growing season.

Family	Suillus inoculation	Suillus seedlings (%)	Suillus mycor. laterals (%)	Total mycor. laterals (%)	Total laterals (#)
1	+	100a	82a	86a	39a
	-	4d	5bc	22b	33b
2	+	100a	78a	80a	34ab
	-	0d	1c	34b	28c
3	+	44c	16b	29b	28c
	-	4d	2c	32b	34ab
4	+	76b	73b	76a	33b
	-	0d	0c	41b	27c

1. Means values in the same column with a different letter are significantly different ($P \leq 0.05$).

Table 2. Ectomycorrhizae development of seedlings inoculated with *S. luteus* after lifting (September, Year 2).

Family	Inoculated	Suillus seedlings (%)	Ectomycorrhizal laterals Suillus (%)	Ectomycorrhizal laterals Total (%)
1	+	92a[1]	84a	89a
	-	6a	2d	54c
2	+	100a	81a	93a
	-	4d	7d	68b
3	+	66c	35c	52c
	-	0d	0d	52c
4	+	80b	69b	82a
	-	4d	10d	59bc

[1] Means values in the same column with a different letter are significantly different ($P \leq 0.05$).

Evaluation of seedling root systems after the second growing season showed that *S. luteus* was persistent in the nursery (Table 2). However, the quantity of *S. luteus* root system colonization declined slightly in year 2. *Suillus luteus* was successfully reisolated from 23% of short roots examined across all treatment conditions. Seedlings in family 3 developed the fewest ectomycorrhizal laterals, regardless of inoculation treatment. Fruiting bodies of *S. luteus* were observed in several replications of the inoculated plots in year 2.

Seedling root and shoot morphology was significantly influenced by both *S. luteus* ectomycorrhizae and family (Table 3). In families 1 and 2, inoculation with *S. luteus* imparted significant increases in seedling height compared with control plants. Inoculation with *S. luteus* also significantly increased seedling dry weight and leaf area in family 2. In contrast, seedlings in families 3 and 4 did not consistently respond to *S. luteus* inoculation. Family 3 seedlings developed the least ectomycorrhizae and, in general, did not respond to the inoculation treatment. Evaluation of seedling foliage did not show significant differences in nitrogen and phosphorus content due to either *S. luteus* inoculation or family.

Discussion

Vegetative inoculum of *S. luteus* was a suitable

Table 3. Morphology and foliage nutrient content of 2-0 seedlings inoculated with *S. luteus* after lifting (September, Year 2).

Family	*Suillus luteus* inoculation	Shoot length (cm)	Total dry weight (g)	Root dry weight (g)	Leaf area (cm^2)	Foliage nutrient content (%) N	Foliage nutrient content (%) P
1	+	24.4c[1]	8.0cd	4.9bc	284bc	2.0	1.1
	-	13.5e	7.2d	5.0abc	275de	1.9	1.0
2	+	26.4bc	11.1a	5.5ab	297ab	2.1	1.1
	-	21.2d	10.5ab	5.9a	283cd	2.2	1.o
3	+	23.8cd	8.5c	4.8bc	269e	2.0	1.3
	-	24.7c	9.2	5.4ab	276d	2.0	0.9
4	+	28.8ab	8.2c	4.0cd	301a	1.9	1.0
	-	29.7a	7.2d	3.6d	293abc	1.8	1.0

[1] Means values in the same column with a different letter are significantly different ($P \leq 0.05$).

form of inoculum for early development of ectomycorrhizae on northern red oak seedlings in a northern Michigan nursery. Following soil fumigation, thorough mixing of inoculum into the seedling root zone resulted in significant ectomycorrhizal colonization of primary lateral roots. Inoculum mixing apparently increased the opportunity for lateral root contact with the vegetative mycelium (10,11,23). Previous reports have suggested that some species or isolates of *Suillus* cannot withstand the mechanical manipulation during inoculum preparation and soil infestation (1,2,30). However, ease of isolation, rapid growth in culture, and persistence in adverse soil conditions may increase the utility of selected *Suillus* species (30).

Three of four families (1,2 and 4) developed significant amounts of ectomycorrhizae, while family 3 formed relatively little. The inability of some oak hosts to form ectomycorrhizae with host-specific or host-general fungal symbionts has been reported previously but not explained (13,20,21). No correlation was apparent in the present study between the number of primary lateral roots (potential sites for fungal colonization) and ectomycorrhizal formation. Previous studies have indicated a host genetic influence on ectomycorrhizal colonization of conifers (7,14).

Early seedling development of ectomycorrhizae by *S. luteus* resulted in significant increases in seedling total dry weight. Dixon et al. (13) observed a similar growth increase in container-grown white and black oak seedlings following inoculation with this isolate of *S. luteus*. In contrast, Dixon et al. (13) and Marx (21) reported that isolates of *S. cothurnatus*, *S. pinorigidus* , *S. hirtellus*, and *S. granulatus* failed to form ectomycorrhizae with various oak hosts under a range of environmental conditions. Oak seedling response to inoculation may thus depend on the *Suillus* isolate and the inoculation techniques used as well as the host *Suillus* species combination (26,30).

Soil fumigation delayed ectomycorrhizal colonization of noninoculated seedlings. Although indigenous ectomycorrhizal fungi eventually invaded the control plots, significant quantities of ectomycorrhizae were not observed on seedlings until the end of the first growing season. Delayed ectomycorrhizal colonization of oak seedlings can be lead to nutritional deficits and stunted seedlings (1,2,11,23). However, seedling foliage nitrogen and phosphorus content was not deficient in the present study.

Fertilization with ammonium sulphate did not suppress ectomycorrhizal colonization. Several authors have reported that soil nitrogen fertilization, especially NO_3 above 100 µg/g, reduced ectomycorrhizal colonization of white, southern red, northern red, and black oak seedling by *P.*

tinctorius (4,6,29). Dixon et al. (9) attributed the reduction in ectomycorrhizal colonization by nitrogen fertilization to reductions in root soluble carbohydrates. Beckjord et al. (4,6) speculated that oak ectomycorrhizal formation may be influenced by host-fungal symbiont tolerance to NO_3 and soil NO_3-NH_4 ratios. Fertilization with ammonium nitrate did not reduce ectomycorrhizal colonization of conifers by various symbionts in previous studies (22,23).

The relatively short growing season, cool soil temperatures, and cultural practices employed in the Toumey nursery did not impede ectomycorrhizae formation. Previously, inoculation of conifers with vegetative inoculum of the fungal symbiont *P. tinctorius* in Toumey nursery was relatively unsuccessful (22). These observations suggest the need for further testing of fungal species that are tolerant of freezing ambient temperatures and dry soil conditions (29).

The occurrence of *Hebeloma*, *Inocybe*, *Laccaria*, and *Thelephora* fruiting bodies suggests that ectomycorrhizal fungi can adapt to freezing ambient temperatures and dry soil conditions (1,2,15). Artificially introduced *S. luteus* was persistent throughout two growing seasons. However, conifer and hardwood seedling root systems from nurseries in northern USA have shown a uniformly low level of ectomycorrhizae colonization following lifting (1,2,25,29), especially when

Table 4. Fungal symbionts compatible with bare-root and container grown oak (*Quercus*) seedlings.

Symbiont	*Quercus* host	container (c) or bare-root (br)	growth response (+,0,-)	reference
Cenococcum geophilum	*Q. alba*	c	0	13
	Q. robur	c	+	13,15
	Q. rubra	br	+,0	5,21
	Q. venutina	c,br	0	10,11,13,27
Hebeloma crustuliniforme	*Q. robur*	br	+	15
Pisolithus tinctorius	*Q. alba*	br	+	8,20
	Q. palustris	c	+	18
	Q, rubra	c,br	0,+	21,28
	Q. velutina	c,br	+	10,11,13,27
Rhizopogon sp.	*Q. rubra*	br	0	15
Scleroderma auranteum	*Q. alba*	c	+	3
	Q. rubra	c	+	3
Suillus granulatus & *S. luteus*	*Q. alba*	c	+	13
	Q. velutina	c	+	13
	Q. robur	c	+	13,15
	Q. rubra	c,br		21
Thelephora terrestris	*Q. alba*	br	0	13,15
	Q. rubra	c,br	0	15

compared with reports for various tree genera from southeastern regions of North America (23,29). Moreover, symptoms of ectomycorrhizal deficiency, such as stunted seedlings and phosphorus deficiency, are relatively common in the northern USA (1,2,17,29).

The overall survival and juvenile growth of oak seedlings in the nursery and following outplanting may be improved if ectomycorrhizae formation is adequate (Table 4). A number of ectomycorrhizal fungi appear to be useful in artificial inoculation programs including species of *Cenococcum*, *Hebeloma*, *Pisolithus*, *Rhizopogon*, *Scleroderma*, *Suillus* and *Thelephora*. Oak seedlings generally respond positively to inoculation with ectomycorrhizal fungi in nurseries and container systems under a range of soil and climate conditions and cultural practices. Further testing of fungal symbionts with various hosts and cultural practices is necessary before specific nursery prescriptions can be made.

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Résumé. Un inoculum végétatif d'ectomycorhize, *Suillus luteus*, était minutieusement mélangé à un sol fumigé de culture et des semis de quatre familles de chêne rouge d'Amérique étaient évalués une et deux années après en regard du développement d'ectomycorhizes, de la croissance et de la nutrition. À la fin de l'année 1, les semis traités étaient inoculés avec succès par *S. luteus*, mais le pourcentage de réussite variait significativement d'une famille à l'autre. *Suillus luteus* persistait sur les racines latérales pour deux ans. Deux des quatre familles de semis inoculées avec *S. luteus* étaient, de manière significative, plus grandes en taille que les plants-contrôle. Ces résultats suggèrent qu'une symbiose fongique avec le *S. luteus* peut être introduite avec succès dans les pépinières et que le développement d'ectomycorhizes améliore la croissance des semis de chêne rouge d'Amérique.

Zusammenfassung. Ein vegetatives Inoculum des Ectomykorrhizapilzes *Suillus luteus* wurde gründlich mit begaster Baumschulerde vermischt. Roteichen-Sämlinge von vier Familien wurden ein bis zwei Jahre später hinsichtlich einer Ectomykorrhizaentwicklung, Wachstum und Ernährung beurteilt. Am Ende des ersten Jahres waren einige der behandelten Sämlinge erfolgreich mit *S. luteus* beimpft, aber der Prozentsatz variierte deutlich von einer Familie zur anderen. *S. luteus* enverblieb auf den Seitenwurzeln für zwei Jahre. Bei zweien der vier Sämlingsfamilien waren die mit *S. luteus* beimpften Pflanzen bedeutend größer als die Kontrollen. Diese Ergebnisse deuten an, daß der Pilzsymbiont *S. luteus* erfolgreich in Baumschulen eingeführt werden kann, und daß frühe Ectomykorrhizaentwicklung das Wachstum von Roteichensämlingen verbessert.