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Growth Response of Pinus rigida x P. taeda to Mycorrhizal Inoculation and Efficiency of Pisolithus tinctorius at Different Soil Texture and Fertility with Organic Amendment¹

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리기테다 소나무의 菌根 接種 反應과 土壤肥沃度에 따른 모래밭 버섯의 効果 및 그 生態學的 意味'

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ABSTRACT

Potted, germinating *Pinus rigida* x *P. taeda* seedlings were inoculated with *Pisolithus tinctorius* (Pt) ectomy-corrhizal fungus to test the effectiveness of Pt in relation to organic amendment and changes in soil fertility and soil texture. Pt was cultured as mycelia in vermiculite-peat moss mixture with nutrients and added to sterilized pot soils with or without organic amendment (fully fermented compost) at three soil texture levels (sand, loamy sand, and sandy loam) in a factorial design. Plants were grown in a greenhouse for 4 months and harvested to compare their growth with non-mycorrhizal plants and plants infected by natural fungi.

Regardless of soil texture, soil fertility, or organic amendment, seedlings inoculated with Pt were better in dry weight and height than non-mycorrhizal plants or those infected by natural fungi. An exception was observed in the most fertile soil (0.075% N and 1.32% organic matter content in sandy loam with organic amendment), where non-mycorrhizal plants were slightly bigger (8%) and heavier (18%) than Pt-inoculated plants. In over-all average, Pt-inoculated seedlings were 30% taller and 107% heavier than those infected by natural fungi and 31% taller and 60% heavier than non-mycorrhizal plants. Growth stimulation of seedlings by Pt was more pronounced in less fertile sand soil when organic was not amended.

Mycorrhizal frequency of Pt (% of mycorrhizal root tips) was reduced to about half (from 84 to 33% in sandy loam and from 77 to 40% in loamy sand) by organic amendment, while that of natural fungi was not significantly affected. Severe nitrogen deficiency was observed in the needles of non-mycorrhizal plants (1.38% N), while both Pt-inoculated plants (1.68% N) and those infected by natural fungi (1.89% N) did not develop symptom, suggesting an active role of mycorrhizae in absorption of soil nitrogen. Top to root ratio increased with organic amendment to non-mycorrhizal plants, but was not significantly affected by fungal treatment.

It was concluded from this study that relative effectiveness of Pt was determined by soil fertility. Organic amendment to less fertile sand soil increased effectiveness of Pt, while the same amendment to more fertile

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loamy sand and sandy loam decreased effectiveness of Pt. Benefits of Pt mycorrhizae would be expected most either when organic was not added to the soil, or when soil nutrients were not abundant.

Key words: Mycorrhizal inoculation, Pisolithus tinctorius, Organic amendment, Pinus rigida x P. taeda.

要 約

外生菌根을 形成하는 모래발버섯군(Pisolithus tinctorius)(Pt)을 對象으로 土性의 變化의 堆肥의 添加로 因한 土壤肥沃度의 變化에 따른 共生菌으로써의 生長促進效率을 調査하였다. Pt菌을 vermiculite peat moss - 營養液에 菌絲形態로 培養하여 세가지 土性(砂土, 壤質砂土, 砂質壤土), 堆肥의 添加有無, 菌根菌의 種類(Pt菌, 天然 菌根菌, 無菌根)에 따른 要因試驗設計에 맞추어서, 消毒된 흙 속에 接種하였다. 接種된 흙을 4 ℓ 容量의 플라스틱 花盆에 담고 4개의 리기테다소나무(Pinus rigida×P.taeda) 種子를 播種하고 温室에서 四個月間 生育시켰다. 收穫後에 處理間에 苗高, 乾重量, 菌根形成率, 窒素含量, T/R率을 調査하였다.

土性, 土壤肥沃度, 堆肥添加有無에 關係없이, Pt로 接種된 苗木은 天然菌根菌으로 (土壤 消毒없이 天然的으로 形成된 菌根)接種된 苗木이나 無菌根苗木(土壤消毒만 實施)보다 苗高生長과 乾重量에서 훨씬 더 컸다. 그러나 가장 土壤肥沃度가 높은 土壤(堆肥가 添加된 砂質壤土, 室素 0.075%, 有機物 1.32%)에서는 無菌根苗木이 Pt苗木보다 苗高에서 8%, 乾重量에서 18% 더 좋았다. 全体 平均으로 볼 때, Pt苗木은 天然菌根苗木보다 苗高에서 30%, 乾重量에서 107% 더 컸으며, 無菌根苗木보다 苗高에서 31%, 乾重量에서 60% 더 컸다. 土壤肥沃度가 낮고 堆肥가 添加되지 않았을 때, Pt菌에 依한 生長促進效果가 더 크게 나타났다.

菌根形成頻度는 堆肥添加로 Pt의 경우에 折半으로 (砂質壤土의 境遇에 84에서 33%로, 壤質砂土의 境遇에 77에서 40%로) 줄었으나, 天然菌根菌의 境遇에는 줄지 않았다. 無菌根苗木은 甚並 窒素缺乏現象(1.38%N)을 일으킨 反面에, Pt接種苗木(1.68%N)과 天然菌根苗木(1.89%N)은 正常的이었다. 이로 미루어 보아서 菌根菌은 土壤內 窒素의 吸收量 促進한다고 생각된다. T/R率은 堆肥添加로 因하여 增加하였으나,菌根菌의 種類나 그 存在有無로 因하여 影響을 받지 않았다.

모래발버섯군의 生長促進效率은 土壤의 肥沃度에 依하여 決定된다고 結論지을 수 있다. 즉 肥沃度가 낮은 砂質土에 堆肥를 添加하면 Pt의 效率이 크게 나타나지만, 肥沃度가 더 높은 砂質壤土에 堆肥를 添加하면 Pt의 效率이 적게 나타난다. 모래발버섯군의 利點은 堆肥를 添加하지 않을 境遇와 上壤의 肥沃度가 높지 않을 때 더 크게 나타날 것이라고 생각된다.

INTRODUCTION

In natural environment most plant roots maintain a symbiotic relationship with certain soil fungi, which is known as mycorrhizae. The widespread occurrence of mycorrhizae in nature has been credited for ecological significance of this unique symbiosis in nutrient absorption, nutrient cycling, water relation, interaction with other soil microorganisms, and protection of roots from extreme soil conditions such as high temperature, low pH, and toxic substances (Lee et al., 1983). Knowledge of mycorrhizae has been applied to practical phases of agriculture and forestry

(Schenck, 1982). For example, ecto- and endomy-corrhizal fungi can be cultured in large quantity and inoculated to host plants to promote survival, growth, disease resistance, and maximum utilization of applied fertilizers.

Recently an ectomycorrhizal fungus *Pisolithus* tinctorius (Pt) has been successfully used to stimulate growth of pine species (Marx et al., 1977; Lee and Koo, 1983) and oaks (Marx, 1979; Dixon et al., 1981). The benefits of this fungus Pt were also shown in reclamation sites of coal spoils and copper mine (Berry, 1982; Berry and Marx, 1978). Schramm (1966) observed extensive mycelial strands and fruiting bodies of Pt in anthracite mine. It is postulated that Pt has adapted to poor soil

conditions (Marx and Artman, 1978) to compete effectively with other mycorrhizal fungi under harsh conditions.

The purposes of this paper were to test whether Pt responded to organic amendment which resulted in increase in soil fertility, especially nitrogen level and to examine effectiveness of Pt in different soil texture. The performance of Pt was compared with that of naturally occurring fungi and non-mycorrhizal plants.

MATERIALS AND METHODS

Experimental Design

This study was conducted in a greenhouse using potted Pinus rigida x P. taeda seedlings and employed a 3 x 3 x 2 factorial design. The three factors to be tested were fungal type, soil texture, and soil fertility. The first factor was three fungal types: 1) "Pt" added to pots after soil sterilization, 2) "natural fungi" (no soil sterilization or inoculation involved), and 3) "no fungi" added after soil sterilization. The second factor was three levels of soil texture: 1) sand, 2) loamy sand, 3) sandy loam. The third factor involved two levels of soil fertility manipulated by organic amendment: 1) organic (fully fermented compost) amended, and 2) no organic amended. A total of 18 treatment combinations (3 x 3 x 2) were recognized in this design. Ten poss with four seedlings each were assigned for each treatment.

Culture of Ectomycorrhizal Fungi

Pisolithus tinctorius (Pt) #250 was obtained as

mycelium from the Institute for Mycorrhizal Research and Development (USDA Forest Service) in Athens, Georgia, U.S.A. and cultured for about 4 months in glass bottles containing vermiculite, peat moss and modified Melin-Norkrans' (MMN) solution (Marx, 1969). Sucrose in the MMN medium was replaced by glucose as suggested by Marx and Bryan (1975). Preparation of the inoculum was the same as that described by Lee and Koo (1983).

Soil Preparation

Three levels of soil texture were prepared by mixing field soil with sand at different ratio. The field soil was heavy brown soil which had not been cultivated for several years. The three levels of soil texture were sand, loamy sand, and sandy loam based on USDA soil taxonomy system (Anonymous, 1975). Fully fermented compost (a mixture of farm manure and grasses) was used to adjust soil fertility to two levels (organic amended and unamended) without changing soil textural classes.

Table 1 shows chemical and physical properties of prepared soil. The pH of the soils ranged from 5.6 to 7.3. Total nitrogen and organic matter contents increased about ten fold after addition of both field soil and organic to unamended sand. In contrast, available phosphorus and potassium content changed about three fold from 21.8 to 61.6 ppm and from 0.31 to 0.92 me/100g, respectively.

Inoculation and Seeding

About 41 of prepared soil was placed in each plastic pot, and sterilized by steaming at 100°C for three hours. For "Pt" treatment, 200 ml of live

Table 1. Physical and chemical properties of soils prepared for three levels of soil texture and for two levels of soil fertility. Pure sand, field soil, and compost (organic amendment) were mixed at different ratio to produce desired texture and fertility level.

Soil texture	Organic pH		Total N	Organic	P	К	Ca	Mg	Particle size (%)		
Son texture	amendment	1:5	(%)	matter(%)	(ppm)	(me/100g)	(me/100g)	(me/100g)	Sand	Silt	Clay
Sand	No	7.3	0.007	0.11	21.8	0.31	8.66	0.77	94.6	1.4	4.0
	Yes	6.6	0.045	0.55	48.9	0.89	8.93	1.58	88.2	5.8	6.0
Loamy sand	No	7.1	0.028	0.39	41.5	0.37	8.66	0.84	79.2	11.8	9.0
	Yes	6.7	0.056	0.66	57.6	0.76	10.03	1.61	81.5	8.9	9.6
Sandy loam	No	5.6	0.040	0.77	59.4	0.54	9.08	1.39	63.1	19.9	17.0
	Yes	6.2	0.075	1.32	61.6	0.92	9.54	1.82	72.8	13.6	13.6

inoculum of vermiculite-peat moss-mycelium mixture was added to each pot and mixed thoroughly with soil. For "no fungus" treatment, same amount of autoclaved inoculum was added to sterilized soil. For "natural fungi" treatment, unsterilized soil was used without artificial fungal inoculation.

Seeds of *Pinus rigida* x *P. taeda* hybrid were surface-sterilized in a 1% H₂O₂ solution and ten seeds were sown in each pot. After successful germination, seedlings were thinned out to leave four plants in each pot. Plants were grown in a greenhouse for four months. No fertilizer or biocides were used during the experimental period.

Harvest and Measurements

Height of each seedling was measured just before the harvest. Entire shoots and roots were lifted to measure top/root ratio. Mycorrhizal frequency was determined by counting mycorrhizal root tips under a dissecting microscope, Mycorrhizal tips were differentiated from non-mycorrhizal tips by criteria described by Wilcox (1968). The harvested plants were dried in an oven at 80°C for three days for dry weight determination and total nitrogen content was measured by micro-Kjeldahl method.

RESULTS

Effects of Fungal Type on Growth of Host Plants

Table 2 shows dry weight and height growth of Pinus rigida x P. taeda seedlings either inoculated with Pt, induced to form mycorrhizae with natural fungi, or without any mycorrhiza. In all three levels of soil texture, Pt treatment produced taller and heavier seedlings than natural fungi or no fungus treatment. Compared with natural fungi, Pt increased dry weight of inoculated seedlings by 107% in average (0.91g versus 0.44g), and height growth by 30% (14.0 cm versus 10.8 cm). Pt inoculated seedlings were also bigger and heavier than nonmycorrhizal plants. For example, Pt-inoculated plants were 2.4 (0.53 versus 0.22g) to 4.6 times (0.97 versus 0.21g) heavier than non-mycorrhizal plants when organic was not amended. An exception was observed in the most fertile soil with 0.075% N and 1.32% organic matter (sandy loam with organic amendment), where non-mycorrhizal plants were slightly bigger (8%) or heavier (18%) than Pt-inoculated plants. Natural fungi were generally ineffective in growth stimulation of host plants. Particularly when organic was amended, natural fungi performed more poorly than no fungus treatment. Non-mycorrhizal plants penformed poorly perticularly when organic was not added to the soil.

Effects of Soil Texture on Performance of Pt

A soil texture change from sand to sandy loam

Table 2. Oven-dry weight (g, D.W.) and height growth (cm) of potted *Pinus rigida x P. taeda* seedlings inoculated with either *Pisolithus tinctorius* (Pt), natural fungi, or no fungus and grown for four months at three levels of soil texture with or without organic (well-fermented compost) amendment. Ten pots with four seedlings each were assigned for each treatment and each number is an average of 40 observations.

Call tarreture	Organic		Pt	No	fungus	Natural fungi	
Soil texture	amendment	D.W.*	Height	D.W.*	Height	D.W.*	Height
Sand	No	0.53	12.4	0.22	6.6	0.23	6.6
	Yes	0.73	13.4	0.62	12.2	0.35	9.1
Loamy sand	No	0.97	12.8	0.21	6.0	0.52	12.0
	Yes	0.92	15.4	0.73	13.4	0.43	11.4
Sandy loam	Nol	1.34	14.3	0.45	9.5	0.60	13.7
	Yes	0.99	15.4	1.17	16.6	0.51	12.0
Average		0.91	14.0	0.57	10.7	0.44	10.8

^{*:} In dry weight data statistically significant (at 1% level) interactions were observed between fungal type (FT) and soil texture (ST) between FT and organic amendment (OA), between ST and OA, and among FT, ST, and OA.

increased total nitrogen in soil about six fold, available phosphorus about three fold and organic matter content seven fold, and decreased soil pH from 7.3 to 5.6 as shown in Table 1. Accordingly plant growth was better in sandy loam than in sand. Pt performed better than natural fungi or no fungus treatment in all three types of soil texture tested in this experiment. Particularly largest height growth stimulation by Pt was observed (12.4 versus 6.6cm) in sand soil without organic amendment, where nutrient contents were lowest among six levels of soil fertility.

Effect of Organic Amendment on Performance of Pt

Organic amendment increased soil nitrogen content by two to six times and available phosphorus by almost none to about two times depending on the soil textural levels (Table 1). In Pt treatment, organic amendment slightly increased height growth in all three levels of soil texture. However, dry weight in Pt treatment was decreased by organic amendment to loamy sand and sandy loam. In natural fungi treatment, organic amendment to sand increased both height and dry weight, while organic amendment to loamy sand and sandy loam had an adverse effect on height growth and dry weight. In contrast to Pt and natural fungi treatment, nonmycorrhizal plants (no fungus treatment) responded to organic amendment. Both dry weight and height

were increased by more than two fold by organic amendment.

Root collar diameter was not measured in this experiment. However, it was clear from the data that in Pt treatment sandy loam without organic amendment produced shorter (14.3cm) and heavier (1.34g) seedlings than that with organic amendment (15.4cm and 0.99g), suggesting bigger root collar diameter in the former.

Mycorrhizal Frequency, Nitrogen Content, and Top/Root Ratio

Table 3 shows frequency (%) of mycorrhizal root tips. Regardless of fungal types, seedlings grown in sand soil had lower mycorrhizal frequency than those in loamy sand and sandy loam. Organic amendment showed more pronounced effect on mycorrhizal formation by Pt than by natural fungi. In Pt treatment, organic amendment suppressed mycorrhizal formation in all three levels of soil texture. In sandy loam without organic amendment, for example, 83.6% of total root tips formed mycorrhizae with Pt, while only 32.9% of root tips were mycorrhizal when organic was amended. Berry and Marx (1977) also observed decrease in percent of mycorrhizal short roots with increasing amount of organic amendment. In natural fungi treatment, however, organic amendment slightly increased mycorrhizal frequency in sand and loamy sand, but slightly decreased frequency

Table 3. Nitrogen content (% of dry weight) and mycorrhizal frequency (M. F., % of mycorrhizal root tips) of potted *Pinus rigida x P. taeda* seedlings inoculated with either *Pisolithus tinctorius* (Pt), natural fungi, or no fungus and grown for four months at three levels of soil texture with or without organic (well fermented compost) amendment. Ten pots with four seedlings each were assigned for each treatment and each number is an average of 40 observations.

	Organic		Pt	N	o fungus	Natural fungi	
Soil texture	amendment	N	M.F.	N	M.F.	N	M.F
Sand	No	1.74	47.4	1.33	0	2.00	29.2
ĺ	Yes	1.45	20.7	1.37	0	1.92	38.8
Loamy sand	No	1.50	76.6	1.32	0	1.81	53.3
	Yes	1.99	40.0	1.44	0	2.06	58,2
Sandy loam	No	1.55	83.6	1.62	15.5*	1.68	79.4
	Yes	1.87	32.9	1.21	0	1.84	67.5
Average		1.68	50.2	1.38	2.6	1.89	54.4

^{*:} A few pots were contaminated with unknown fungi.

Organic Fungal type Soil texture amendment Pt No fungus Natural fungi No 1.45 1.33 1.53 Sand Yes 1.59 1.58 1.39 No 1.64 1.50 1.68 Loamy sand Yes 1.73 1.79 2.06 No 177 1.32 2.10 Sandy loam Yes 1.74 1.98 1.75 1.58 Average 1.65 1.75

Table 4. Top/root ratio of potted *Pinus rigida x P. taeda* seedlings inoculated with either *Pisolithus tinctorius* (Pt), natural fungi, or no fungus and grown for four months at three levels of soil texture with or without organic amendment. Ten pots with four seedlings each were assigned for each treatment, and each number is an average of 40 observations.

in sandy loam.

Nitrogen content in the needles is also shown in Table 3. Plants in natural fungi treatment had higher nitrogen contents than two other fungal treatments. This high nitrogen concentration appears to be related to slow growth of the treated plants as shown in Table 2. On the other hand non-mycorrhizal plants had lowest nitrogen contents and showed nitrogen deficiency, even though they grew as slow as those plants in natural fungi treatment. Exceptionally fast height growth of non-mycorrhizal plants in sandy loam with organic amendment (16.6cm in Table 2) was associated with lowest nitrogen content (1.21%) in Table 3. In Pt treatment, organic amendment in loamy sand and sandy loam increased nitrogen content in the tissue, even though mycorrhizal frequency was reduced by organic amendment.

Table 4 shows top to root ratio (T/R) of the treated plants. Organic amendment either increased or decreased the ratio, depending on soil texture and fungal type. Fungal treatment did not result in significant change in T/R ratio. In general, plants grown in sandy loam had higher T/R ratio than those in sand of low fertility.

DISCUSSION

It was clearly shown in the present study that Pinus rigida x P. taeda seedlings inoculated with Pisolithus tinctorius (Pt) grew more than two times faster in dry weight than those infected by natural fungi. The Pt-inoculated plants outperformed non-mycorrhizal or naturally infected plants grown in sand, loamy sand, and sandy loam with or without organic amendment. However, relative performance of Pt (dry weight increase of host) appeared to be determined by soil fertility. Organic amendment to less fertile sand soil increased effectiveness of Pt, while the same amendment to more fertile loamy sand and sandy loam decreased effectiveness of Pt. It suggested that benefits of Pt mycorrhizae would be expected most when organic is not added to the soil, and when soil nutrients are not abundant.

Pisolithus tinctorius has been postulated to have adapted to poor soil conditions in natural environments (Marx and Artmen, 1978). The better performance of Pt in less fertile soil in the present experiment also supports their observation. However, seedlings inoculated with Pt were bigger and heavier in the five levels of soil fertility than seedlings lacking mycorrhiza or infected by natural fungi. Non-mycorrhizal plants grown in most fertile soil (sandy loam with organic amendment) were bigger and heavier than Pt-inocultated plants, suggesting that when total nitrogen in soil was in certain level (0.075% N in the present experiment) Pt failed to stimulate growth of host plants. It is unlikely that pnosphorus was directly involved in determining threshold soil fertility level, because organic amendment to sandy loam slightly changed phosphorus content from 59.4 to 61.6 ppm, and instead changed nitrogen content about two fold (from 0.04 to 0.075%).

Mycorrhizal formation of fine roots with Pt was significantly suppressed by addition of organic material which subsequently increased soil fertility, particulary nitrogen level. Suppression of mycorrhizal formation by high levels of nitrogen was also observed by Menge et al. (1977), Marx et al. (1982) and Marx et al. (1977b). In contrast with Pt's susceptibility to nitrogen level, natural fungi in the present experiment were not significantly affected by organic amendment in their ability to form mycorrhizae.

One of the interesting observations in this experiment is varying nitrogen content in the tissue affected by fungal type and mycorrhizal frequency. In Pt treatment, low mycorrhizal frequency in amended soil was not associated with low nitrogen content in the tissue, suggesting that absorption of nitrogen was not reduced by poor mycorrhizal formation. This observation appears to agree with a well accepted hypothesis that, in contrast to phosphorus, mycorrhizal roots do not facilitate nitrogen absorption but simply absorb readily available nitrogen form in soil solution (Bowen and Smith, 1981). This implies that non-mycorrhizal roots also should absorb nitrogen without difficulty. However, non-mycorrhizal plants in this experiment showed nitrogen deficiency as shown in Table 3. This poor absorption of nitrogen by nonmycorrhizal roots is contradictory to the optimal absorption of nitrogen by Pt-inoculated seedlings with low mycorrhizal frequency, if we accept the suggestion of Bowen and Smith (1981). One possible explanation for the contradiction is that mycorrhizal roots might have an unknown active mechanism for facilitated absorption of nitrogen as for the case of phosphorus.

The better performance of Pt in less fertile or poor soil indicates ecological significance of this fungus in afforestation and reclamation of eroded sites. In the U.S. this fungus has been successfully used for reclamation of acid coal spoils (Marx and Artman, 1979; Berry, 1982) and copper mine

(Berry and Marx, 1978). In addition the beneficial effects of this fungus have been demonstrated in pine nursery (Marx and Bryan, 1975; Marx et al., 1976), containerized seedlings (Marx et al., 1982) and plantation (Marx et al., 1977a; Berry, 1982). The benefits of this fungus are believed to come from its ability to grow vigorously at high soil temperature (Marx and Bryan, 1971; Schramm, 1966), and in soil pH as low as 3.5 (Marx, 1977a). This fungus is also able to stimulate growth of host plants by absorbing nutrients more effectively than other mycorrhizal fungi (Lee and Koo, 1983).

These observations mentioned above and broad host range and worldwide distribution of Pt (Marx, 1977b) suggests the importance of this mycorrhizal fungus in forest ecosystem, especially in nutrient cycling. Fogel (1980) reported that most of the organic input to the decomposition process results from fine root production and that mycorrhizal roots account for 50% of the annual throughput of biomass and for 43% of the nitrogen released annually in a Douglas-fir ecosystem. These transfers were five times larger than the releases from litter fall or litter decomposition. In addition further study is needed to identify the roles of mycorrhizal fungi in maintaining a balance between different microbial populations as suggested by Bowen and Theodorous (1979).

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