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SPECIAL FEATURE: ORIGINAL PAPER

Seed germination and seedling physiology of *Larix kaempferi* and *Pinus densiflora* in seedbeds with charcoal and elevated CO_2

Dongsu Choi · Kobayashi Makoto · Ali M. Quoreshi · Laiye Qu

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Abstract We investigated the effect of ectomycorrhizal colonization, charcoal and CO_2 levels on the germination of seeds of *Larix kaempferi* and *Pinus densiflora*, and also their subsequent physiological activity and growth. The seeds were sown in brown forest soil or brown forest soil mixed with charcoal, at ambient CO_2 (360 μmol mol^{-1}) or elevated CO_2 (720 μmol mol^{-1}), with or without ectomycorrhiza. The proportions of both conifer seeds that germinated in forest soil mixed with charcoal were significantly greater than for seeds sown in forest soil grown at each CO_2 level ($P < 0.05$; *t*-test). However, the ectomycorrhizal colonization rate of each species grown in brown forest soil mixed with charcoal was significantly lower than in forest soil at each CO_2 treatment [CO_2] ($P < 0.01$; *t*-test). The phosphorus concentrations in needles of each seedling colonized with ectomycorrhiza and grown in forest soil were greater than in nonectomycorrhizal seedlings at each CO_2 level, especially for *L. kaempferi* seedlings ($P < 0.05$; *t*-test), but the concentrations in seedlings grown in brown forest soil mixed with charcoal were not increased at any CO_2 level. Moreover, the maximum net photosynthetic rate of each seedling for light and CO_2 saturation (P_{max}) increased when the seedlings were grown with ectomycorrhiza at 720 μmol mol^{-1} [CO_2]. Ectomycorrhizal colonization led to an increase in the stem diameter of each species grown in each soil treatment at each CO_2 level. However, charcoal slowed the initial growth of both species of seedling, constraining ectomycorrhizal development. These results indicate that charcoal strongly assists seed germination and physiological activity.

Keywords Ectomycorrhizal colonization rate · Maximum net photosynthetic rate at light and CO_2 saturation (P_{max}) · Growth · Brown forest soil

Introduction

Larix and *Pinus* species are popular in northeast Asia, but serious degradation of these forests has taken place in recent years due to human activity, including fires and timber cutting (Choi et al. 2006; Hytteborn et al. 2005; Koike et al. 2000; Nakamura and Krestov 2005; Qu et al. 2005). This has happened in, for example, the central part of the Korean peninsula, the Far East of Russia, and northeast China (Makoto 2005, 2007b; Choi et al. 2008). Changes to the environment, such as atmospheric CO_2 levels, are also accelerating, and photosynthetic adjustment is often observed in plants (Choi et al. 2006, 2008; Farrar and Williams 1991; IPCC 2000, 2007). It is increasingly important to establish a practical method of forest rehabilitation in such degraded areas. Accelerating the natural regeneration of pine species is a good approach, since it exerts no environmental stress on the land.

D. Choi (✉)
Institute of Symbiotic Science and Technology,
Tokyo University of Agriculture and Technology,
Fuchu, Tokyo 183-8509, Japan
e-mail: choids@cc.tuat.ac.jp

K. Makoto
Graduate School of Agriculture, Hokkaido University,
Sapporo 060-8589, Japan

A. M. Quoreshi
Symbiotech Research Inc., 20/20 Seed Labs Inc.,
#201, 509-11 Avenue, Nisku, AB T9E 7N5, Canada

L. Qu
Eco-Environmental Research Center of CAS, Beijing, China

The most important factor governing natural regeneration in forests is germination and rooting after natural and/or manmade disturbances. After forest fires there is a huge amount of charcoal, which could be important in promoting the establishment of seedlings (Makoto et al. 2007b; Choi et al. 2008). Seed germination initially requires moisture, temperature and oxygen (e.g., Lambers et al. 1998). When a seed takes in water, its respiration increases. If seeds are not supplied with oxygen and a suitable temperature, their viability rapidly declines. Charcoal promotes seed germination by improving soil moisture, soil temperature and physical properties that assist in absorbing oxygen. Charcoal also has large surface area and strongly adsorbs organic compounds (DeBano et al. 1998).

After germination, the seedlings must root and develop root hair as a priority, so as to provide a large surface area through which to absorb water and nutrients. Large numbers of seedlings perish soon after germination, however, and few survive and grow vigorously enough to become established (Barnes et al. 1998). To discover methods of efficient rehabilitation in degraded forests, we should focus on improving the survival and establishment of seedlings at these stages.

Colonization by ectomycorrhiza increases the absorption of essential nutrients and water via hyphal extraction, and improves the tolerance of plants to environmental stresses such as drought, nutrient shortage and toxic metals (Allen 1991; Choi et al. 2005, 2008; Smith and Read 2008). After germination, seedlings "plug into" the network of compatible ectomycorrhizal fungi supported by surviving trees, allowing early ectomycorrhizal formation and establishment (Amaranthus 1994, Nara 2006). Charcoal is also believed to be important in promoting seedling establishment and encouraging mycorrhizal activity that contributes to the growth of host plants (Warnock et al. 2007; Wardle et al. 1998; Hille and Ouden 2005; Makoto et al. 2007a).

Increases in the concentration of atmospheric CO_2, [CO_2], affect the growth and physiological activity of plants (Choi et al. 2008; IPCC 2007). To establish appropriate rehabilitation methods for the foreseeable future, the effect of high [CO_2] on seedling establishment should be taken into account. The germination of seeds of *L. kaempferi* and *P. densiflora* is likely to be accelerated in soil with charcoal, and the growth and development of seedlings is likely to be improved by elevated [CO_2]. The nutrient status in needles may also be improved.

The present study examined the effect of ectomycorrhizal colonization with charcoal on the germination of *L. kaempferi* and *P. densiflora* seeds, and the growth, nutrient and physiological activities of two conifer seedlings grown under increased [CO_2].

Materials and methods

Seed germination

Seeds of the Japanese larch (*Larix kaempferi* Sarg.) and red pine (*Pinus densiflora* Sieb. et Zucc.) were used at the Hokkaido Research Center, Forestry and Forest Products Research Institute (FFPRI), Sapporo, Japan. A total of 180 seeds of each species were maintained at 4°C for ten days of cold treatment. Their surface was then sterilized with 30% H_2O_2 for 20 min, followed by rinsing 4–5 times with sterile deionized water. The seeds were then germinated on sterilized brown forest soil or brown forest soil mixed with charcoal. Brown forest soil, originating from granite, was collected from an organic layer 0–10 cm deep that had been removed from beneath the stands of red pine trees in the town of Shintoku (Hokkaido, Japan). The soil was sieved through a 5 mm mesh immediately after collection so as to homogenize it. The volume of charcoal mixed in the soil was 30%. The collected brown forest soil and charcoal were autoclaved at 121°C for 35 min for sterilize the ectomycorrhizal fungi in the soil.

Ectomycorrhizal colonization

Ectomycorrhizal fungi, namely Diehard Ecto drench (EC)—(*Pisolithus tinctorius* (Pers.) Coker et Couch + *Rhizopogon* spp. + *Laccaria* spp. + *Scleroderma* spp.), were obtained from Horticultural Alliance Inc., East Sarasota, FL, USA. The ectomycorrhizal spores were suspended in 50 ml of distilled water, and this solution was mixed with each soil preparation prior to seed germination.

Growing conditions

The seeds were germinated in six phytotrons at FFPRI with natural sunlight, a day/night temperature range of 26/16°C, and a humidity range of 55–75%. Each seed was allocated at random to CO_2 groups such that half the seeds experienced ambient [CO_2] (360 μmol mol^{-1}) and half experienced elevated [CO_2] (720 μmol mol^{-1}) (Choi et al. 2005).

Measurements of the net photosynthetic rate and stem diameter

The photosynthetic capacity of each seedling was measured using an open gas exchange system (LI-6400, Li-Cor, Lincoln, NE, USA) between 0900 and 1500 hours local time in each CO_2 chamber 18 weeks after germination. The aboveground part was covered from a height

of 5 to 7 cm with a conifer chamber (6400-05, Li-Cor). The leaf temperature was 25°C and the relative humidity was maintained at between 50 and 70%. The needles were allowed to acclimatize to their surroundings for 10 min prior to measurement. The maximum net photosynthetic rate at light and CO_2 saturation, P_{max}, was determined as 1,200 μmol mol^{-1} using light from a cool halogen lamp (WALZ, Effeltrich, Germany) and CO_2 conditions of 1,500 μmol mol^{-1}. After the gas exchange measurement, we measured the needle projection area with an image scanner (FB636U, Canon, Tokyo, Japan) and calculated the net photosynthetic rate per unit needle area.

Following the measurements of the net photosynthetic rate, the stem diameter of each seedling was measured using an electronic micrometer in each CO_2 chamber (CD-15PS, Mitutoyo, Kawasaki, Japan).

Colonization rate of ectomycorrhiza

We observed the root tips and counted both infected and noninfected roots using a microscope (Zeiss Axio Imager A1, Jena, Germany). The colonization rate of ectomycorrhiza was calculated as follows (Choi et al. 2005): colonization rate of ectomycorrhiza (%) = number of ectomycorrhizal root tips/(number of ectomycorrhizal root tips + non-ectomycorrhizal root tips) × 100.

Phosphorus concentration in needles

The seedlings were dried at 60°C for one week after measurements had been taken of the net photosynthetic rate, stem diameter and colonization rate of ectomycorrhiza. The dried samples were ground to fine powder using a sample mill (WB-1, Osaka Chemical Co., Japan). The concentration of phosphorus in the needles was determined using a microwave digestion system (OI Analytical, College Station, TX, USA) and subsequent ICP analysis (IRIS, Jarrell Ash, Franklin, MA, USA) (Thompson and Walsh 1989).

Statistical analysis

Mean values of the germination rate and the ectomycorrhizal colonization rate were compared using the *t*-test. We analyzed P_{max}, the phosphorus concentration in the needles and the stem diameter using the *t*-test and three-way ANOVA for the following effects: CO_2 (C), Soil (S), Ectomycorrhiza (E), and interactions (C × S, C × E, S × E, C × S × E). The *t*-test and three-way ANOVA analyses were performed with SPSS 15.0 software (SPS Institute, Cary, NC, USA).

Results

Germination rate and ectomycorrhizal colonization rate

The germination rate (%) one month after seeds of *L. kaempferi* and *P. densiflora* had been sown in forest soil mixed with charcoal was significantly higher than that for seeds sown in forest soil at each [CO_2] ($P < 0.05$; *t*-test); see Table 1. However, the ectomycorrhizal colonization rates for *L. kaempferi* and *P. densiflora* seedlings grown in forest soil mixed with charcoal were dramatically reduced, to below 25%, and were significantly lower than those obtained without charcoal at each [CO_2] ($P < 0.01$; *t*-test); see Table 2. We did not find any ectomycorrhizal development in the noninoculated seedlings grown at both [CO_2] values, regardless of soil treatment.

Photosynthetic response

Figure 1 shows the maximum net photosynthetic rates under growth conditions of light and CO_2 saturation (P_{max}) for the *L. kaempferi* and *P. densiflora* seedlings grown in each

Table 1 Germination rates (%) one month after *L. kaempferi* and *P. densiflora* seeds had been sown in forest soil or forest soil mixed with charcoal (FS + charcoal) and with the [CO_2] equal to 360 or 720 μmol mol^{-1}

	CO_2 treatment (μmol mol^{-1})	Forest soil	FS + charcoal	*t*-test
L. kaempferi	360	8.33 ± 2.89	16.67 ± 5.77	*
	720	8.33 ± 2.89	15.00 ± 5.00	*
P. densiflora	360	23.33 ± 5.77	33.33 ± 5.77	*
	720	9.33 ± 1.15	18.67 ± 2.31	*

Mean values for three phytotron chambers at each CO_2 treatment ± SE are shown

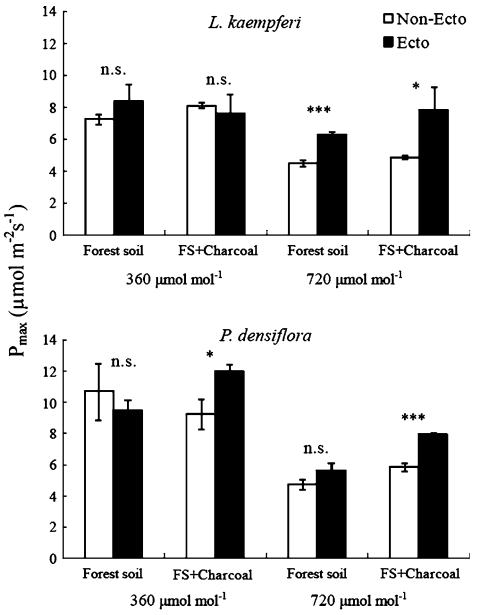
* $P < 0.05$

Table 2 Ectomycorrhizal colonization rates (%) of *L. kaempferi* and *P. densiflora* seedlings in forest soil or forest soil mixed with charcoal (FS + charcoal), either containing ectomycorrhiza or not, after 18 weeks of growth in a [CO_2] of 360 or 720 μmol mol^{-1}

	CO_2 treatment (μmol mol^{-1})	Forest soil	FS + charcoal	*t*-test
L. kaempferi	360	67.32 ± 2.01	11.31 ± 1.25	**
	720	72.14 ± 12.51	13.48 ± 1.44	**
P. densiflora	360	57.80 ± 6.85	11.21 ± 1.06	***
	720	74.47 ± 4.79	23.45 ± 3.51	***

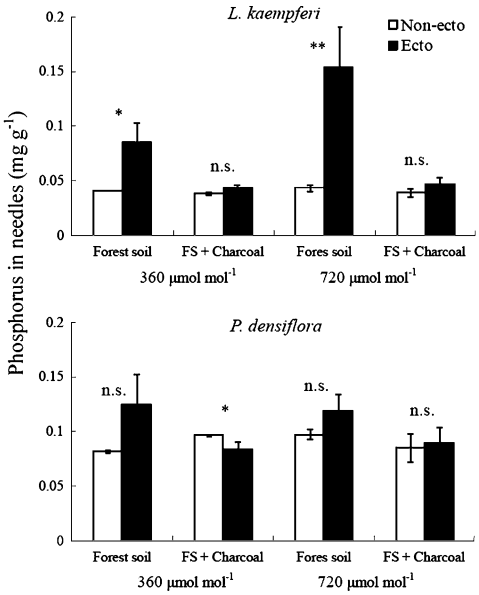
Mean values for three phytotron chambers at each CO_2 treatment ± SE are shown

** $P < 0.01$, *** $P < 0.001$



Three-way ANOVA	C	S	E	C × S	C × E	S × E	C × S × E
L kaempferi	***	n.s.	**	n.s.	n.s.	**	*
P. densflora	***	**	**	n.s.	n.s.	**	n.s.

Fig. 1 Maximum net photosynthetic rate for light and CO_2 saturation (P_{max}) of *L. kaempferi* and *P. densiflora* seedlings in brown forest soil or brown forest soil mixed with charcoal (*FS + Charcoal*) with ectomycorrhiza (*Ecto*) or without ectomycorrhiza (*Non-Ecto*) after 18 weeks of growth under a [CO_2] of 360 or 720 μmol mol^{-1}. Mean of six seedlings grown under each [CO_2] (*C*), soil (*S*) and ectomycorrhiza (*E*) treatment. *Vertical bars* represent the standard error of the mean (±SE). *Asterisks* indicate significant effects according to *t*-test (*in the graph*) or three-way ANOVA (*in the box*). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and *n.s.* means not statistically different ($P \geq 0.05$)



Three-way ANOVA	C	S	E	C × S	C × E	S × E	C × S × E
L kaempferi	**	***	***	*	*	***	*
P. densflora	n.s.	*	*	n.s.	n.s.	**	n.s.

Fig. 2 Phosphorus concentrations of *L. kaempferi* and *P. densiflora* needles in brown forest soil or brown forest soil mixed with charcoal (*FS + Charcoal*) with ectomycorrhiza (*Ecto*) or without ectomycorrhiza (*Non-Ecto*) after 18 weeks of growth under a [CO_2] of 360 or 720 μmol mol^{-1}. Mean of six seedlings grown under each [CO_2] (*C*), soil (*S*) and ectomycorrhiza (*E*) treatment. *Vertical bars* represent the standard error of the mean (±SE). *Asterisks* indicate significant effects according to *t*-test (*in the graph*) or three-way ANOVA (*in the box*). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and *n.s.* means not statistically different ($P \geq 0.05$)

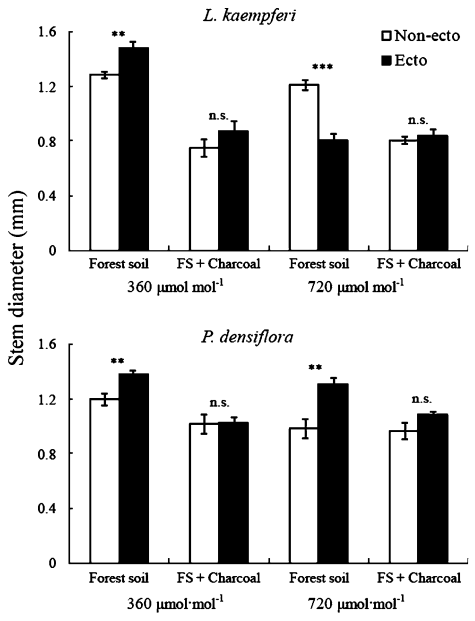
treatment. The value of P_{max} for ectomycorrhizal *L. kaempferi* seedlings grown under a [CO_2] of 720 μmol mol^{-1} at each soil treatment was significantly higher than that for non-ectomycorrhizal (NE) seedlings ($P < 0.05$; *t*-test). The P_{max} values of ectomycorrhizal *P. densflora* seedlings grown in brown forest soil with charcoal at each [CO_2] were significantly higher than those obtained for NE seedlings ($P < 0.05$; *t*-test). The effects on the P_{max} of each species of ectomycorrhizal infection ($P < 0.01$; three-way ANOVA) and CO_2 treatment ($P < 0.001$; three-way ANOVA) were significant. There was a significant interaction between soil and ectomycorrhiza for each species ($P < 0.01$; three-way ANOVA), and a significant interaction among CO_2, soil and ectomycorrhiza for *L. kaempferi* seedlings ($P < 0.05$; three-way ANOVA).

Phosphorus in needles

The phosphorus concentrations in needles of *L. kaempferi* and *P. densiflora* seedlings grown at each [CO_2] (360 and 720 μmol mol^{-1}) in brown forest soil colonized with ectomycorrhiza tended to be greater than those for non-colonized seedlings (Fig. 2). In particular, needles of *L. kaempferi* seedlings colonized with ectomycorrhiza grown in brown forest soil contained significantly more phosphorus than NE seedlings at each [CO_2] ($P < 0.05$; *t*-test). Soil and ectomycorrhiza treatment had significant effects on the phosphorus in needles of *L. kaempferi* seedlings ($P < 0.001$; three-way ANOVA) and *P. densiflora* seedlings ($P < 0.05$; three-way ANOVA), respectively. For phosphorus in needles, there was a significant interaction between soil and ectomycorrhiza for each species ($P < 0.01$; three-way ANOVA). Moreover, there was significant interaction among CO_2, soil and ectomycorrhiza for *L. kaempferi* seedlings ($P < 0.05$; three-way ANOVA).

Growth

Figure 3 shows the stem diameters for *L. kaempferi* and *P. densiflora* seedlings grown in each treatment. In *L. kaempferi* seedlings colonized by ectomycorrhiza, the stem diameter grown in brown forest soil at a [CO_2] of



Three-way ANOVA	C	S	E	C × S	C × E	S × E	C × S × E
L kaempferi	***	***	n.s.	***	***	***	***
P. densflora	**	***	***	**	*	***	n.s.

Fig. 3 Stem diameters of *L. kaempferi* and *P. densiflora* seedlings in forest soil or brown forest soil mixed with charcoal (*FS + Charcoal*) with ectomycorrhiza (*Ecto*) or without ectomycorrhiza (*Non-Ecto*) after 18 weeks of growth under a $[CO_2]$ of 360 or 720 μmol mol^{-1}. Mean of six seedlings grown under each $[CO_2]$ (*C*), soil (*S*) and ectomycorrhiza (*E*) treatment. *Vertical bars* represent the standard error of the mean (±SE). *Asterisks* indicate significant effects according to *t*-test (*in the graph*) or three-way ANOVA (*in the box*). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, and *n.s.* means not statistically different ($P \geq 0.05$)

360 μmol mol^{-1} was significantly greater than for NE seedlings ($P < 0.01$; *t*-test); however, that grown in brown forest soil at a $[CO_2]$ of 720 μmol mol^{-1} was significantly decreased than for NE seedlings ($P < 0.001$; *t*-test). The stem diameters of ectomycorrhizal *P. densiflora* seedlings grown in brown forest soil at $[CO_2]$ values of 360 and 720 μmol mol^{-1} were also significantly greater than those for NE seedlings ($P < 0.01$; *t*-test). The stem diameters of the ectomycorrhizal seedlings of each species (*L. kaempferi* and *P. densiflora*) grown in brown forest soil mixed with charcoal at $[CO_2]$ values of 360 and 720 μmol mol^{-1} were greater than those for NE seedlings, but the difference was not significant. However, we found no tendency with regard to seedling biomass (data not shown). In *L. kaempferi* or *P. densiflora* seedlings, CO_2 and soil treatment had significant effects on the stem diameter ($P < 0.01$; three-way ANOVA). For each species, the stem diameter exhibited significant interactions with CO_2 and soil ($P < 0.01$; three-way ANOVA); with CO_2 and ectomycorrhiza ($P < 0.05$; three-way ANOVA); and with soil and ectomycorrhiza ($P < 0.001$; three-way ANOVA). Moreover, there was a significant interaction among CO_2, soil and ectomycorrhiza for *L. kaempferi* seedlings ($P < 0.001$; three-way ANOVA).

Discussion

In order to achieve forest regeneration after a natural or manmade disturbance, the most important factors are a high rate of seed germination and good survival of seedlings. Germination and survival of seedlings are strongly related to temperature, water, oxygen and photosynthetic rate (Kimmins 2003, Lambers et al. 1998). Addition of charcoal to the soil improves its moisture, temperature and physical properties (DeBano et al. 1998). These properties contribute significantly to the improved germination rates (Table 1) and the increased photosynthetic rates (P_{max}) achieved in some treatments (see Fig. 1).

After germination, seedlings "plug into" the network of compatible ectomycorrhizal fungi supported by surviving trees, making early ectomycorrhizal formation and establishment possible (Amaranthus 1994). The survival and establishment rates of seedlings depend on the rate at which they enter into ectomycorrhizal symbiosis (Janos 1980, 1996). Ectomycorrhizal symbiosis usually functions as an efficient root system for absorbing water and essential nutrients such as nitrogen and phosphate (Choi et al. 2008, Nara 2006, Smith and Read 2008). In this study, however, ectomycorrhizal development in forest soil mixed with charcoal was suppressed to below 25% of its value in forest soil ($P < 0.01$; *t*-test); see Table 2. We conclude that the reduced ectomycorrhizal development in forest soil mixed with charcoal is due to the increase in soil moisture resulting from the addition of charcoal.

The maximum net photosynthetic rate under conditions of light and CO_2 saturation (P_{max}) of NE seedlings grown under a $[CO_2]$ of 720 μmol mol^{-1} is less than that of ectomycorrhizal seedlings for each soil treatment (Fig. 1). Our results also indicate that ectomycorrhizal colonization increases the uptake of nutrient (phosphorus) and water at elevated CO_2 levels, and enhances physiological activity so that there is a significant increase in the growth (stem diameter) of each seedling, except for *L. kaempferi* seedlings grown in forest soil (Figs. 1, 2, 3). Moreover, the stem diameters of *L. kaempferi* and *P. densiflora* seedlings grown in brown forest soil with ectomycorrhizal colonization were much greater than those observed in brown forest soil mixed with charcoal under a $[CO_2]$ of 360 μmol mol^{-1}. The phosphorus concentration in needles of seedlings colonized with ectomycorrhiza and grown in forest soil was greater than that in NE seedlings at each CO_2 level; the increase was particularly significant in *L. kaempferi* seedlings, but the value for seedlings grown in

brown forest soil mixed with charcoal was not greater, even with ectomycorrhizal colonization (Fig. 2).

It has been suggested that rapid and early integration of seedlings into adult ectomycorrhizal root systems has benefits in relation to carbon transfer from donor to receptor trees (Choi et al. 2005; Rouhier and Read 1998, 1999; Simard et al. 1997; Tissue et al. 1996). Charcoal addition usually inhibited ectomycorrhizal development, however, by retaining soil moisture and raising the soil pH. The mechanism of inhibition of ectomycorrhizal colonization is expected to be the inhibition of the signal pathway elucidated by Rutto and Mizutani (2006).

The present results suggest that charcoal is helpful for seed germination and physiological activity, but that it should be applied after ectomycorrhizal symbiosis has been established. How to increase ectomycorrhizal development in forest soil mixed with charcoal so as to increase the survival and establishment rates of seedlings remains to be determined.

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