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# Effects of wood decomposer fungi on tree seedling establishment on coarse woody debris

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A B S T R A C T

Although decomposer fungi have been recognized to play important roles in forest carbon and nutrient cycling as well as soil humus formation, their effects on forest dynamics, such as tree regeneration, are far less well understood than the effects of symbiotic and pathogenic fungi. In this study, I focused on tree regeneration on fallen woody debris, "nurse logs". I examined the effects of wood decomposer fungi on species composition and population densities of tree seedlings (height <50 cm) established on these logs. In an abandoned tract of coppice forest in Honshu, Japan, a thick litter layer had accumulated on the forest floor and seedlings of the small-seeded pioneer tree species *Clethra barbinervis* (Ericales) were found to be preferentially established on rotting fallen logs of the Japanese red pine *Pinus densiflora*. *C. barbinervis* seedling establishment was considerably reduced on soil probably because there were impediments to colonization on the ground, such as the thick litter layer, which was less well developed on logs. In contrast, larger-seeded species such as *Aphananthe aspera*, *Carpinus* spp., *Quercus serrata*, and *Rhus trichocarpa* preferentially established on soil. Characteristics of wood decomposition by fungi varied among logs, and this variability significantly influenced *C. barbinervis* seedling density. Seedling density was significantly higher on brown-rotted logs than that on logs belonging to other decay types. Wood pH was lower in brown-rotted logs than that in logs belonging to other decay types and was negatively correlated with seedling density. Thus, pine coarse woody debris and the functional diversity of wood inhabiting fungi influence the establishment of diverse tree seedlings in this abandoned Japanese coppice forest.



## 1. Introduction

Soil fungi (e.g. symbionts, pathogens, and decomposers) have strong direct and indirect effects on aboveground vegetation dynamics (Bardgett and Wardle, 2010; Van der Heijden et al., 2008). Symbiotic mycorrhizal fungi are crucial agents for plant growth and survival. These fungi improve water and nutrient uptake and boost defenses of host plants against root pathogens (Smith and Read, 2008). In contrast, pathogenic fungi are responsible for mortality and reduced fecundities of individual plants and drive host population dynamics (Gilbert, 2002). In some cases, pathogenic fungi have important roles in the maintenance of local species diversity in natural plant communities (Packer and Clay, 2000). These effects of symbiotic and pathogenic fungi are examples of direct interactions between fungi and plants. The effects on aboveground vegetation dynamics, including forest regeneration, are well researched for both symbiotic (Dickie et al., 2002; McGuire, 2009; Nara, 2006; Nara and Hogetsu, 2004; Perry et al., 1989) and pathogenic interactions (Packer and Clay, 2003; Seiwa et al., 2008; Yamazaki et al., 2009). Decomposer fungi may also influence aboveground plant regeneration through indirect interactions because they play an important role in the breakdown and transformation of organic matter to soil humus. Furthermore, decomposer fungi create safe sites (e.g. decayed logs) for tree seedling establishment (Bardgett and Wardle, 2010; Harmon et al., 1986), but little is known about the mechanisms of decomposer fungal activity that influence plant regeneration, especially of trees.

Coarse woody debris (CWD) is a major decay substrate and energy source for forest decomposer fungi (Rayner and Boddy, 1988; Swift et al., 1979). Wood decomposition by fungi is classified into different decay types such as white-rot, brown-rot, and soft-rot, which indicate lignocellulose decomposition capabilities of the different fungal species (Eaton and Hale, 1993). Because decomposition of lignocellulose is a key factor controlling soil humus formation on the forest floor (Stevenson, 1982), decay type has significant effects on species composition of organisms in soil detritus-based food webs such as bacteria (Folman et al., 2008; Jergensen et al., 1989), ectomycorrhizal fungi (Tedersoo et al., 2008), termites (Cornelius et al., 2002), and beetle larvae (Araya, 1993; Wardlaw et al., 2009) that inhabit dead wood. Wood

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chemical properties including pH and organic content may control communities of organisms in woody debris (Jergensen et al., 1989). Since soil food web properties have feedback effects on above-ground plant growth and community composition (Bardgett and Wardle, 2010), I postulated that wood decay type would also influence plant seedling establishment on fallen logs via altering physicochemical and biotic conditions of logs.

Heterogeneity of forest understory microsites is critically important for seedling colonization by various plant species and for the determination of subsequent forest structure (Nakashizuka, 2001). Among microsites on forest floors, "nurse log" CWD provides important safe sites for seedling establishment in various forest ecosystems such as boreal and subalpine (Doi et al., 2008; Harmon and Franklin, 1989; Iijima and Shibuya, 2010; Narukawa and Yamamoto, 2003; Sugita and Nagaike, 2005; Yano and Shibuya, 2010), temperate (Bellingham and Richardson, 2006; Christie and Armesto, 2003; Heinemann and Kitzberger, 2006; Papaik and Canham, 2006), and tropical woodlands (Sanchez et al., 2009; Santiago, 2000; Van der Meer et al., 1998). Properties of logs, such as diameter (Takahashi, 1994), moss cover (Iijima and Shibuya, 2010; Nakamura, 1992), and decay class (Doi et al., 2008; Mori et al., 2004; Takahashi et al., 2000) influence seedling establishment on logs. However, effects of functional differences among wood decomposer fungi on seedling establishment have yet to be reported.

Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) is a dominant canopy tree species in temperate secondary forests of Japan. The pine wilt disease has killed many adult pine trees over recent decades (Takemoto and Futai, 2008), resulting in accumulation of substantial quantities of pine CWD on forest floors (Kato and Hayashi, 2006). Evaluations of the roles of pine CWD in forest regeneration and maintenance of biodiversity in subsequent forest recovery process are particularly relevant at present. In the present study, I particularly focused on (1) seedling species composition and densities on pine logs, (2) the effects of diverse log properties, including wood decay type, on seedling densities of the most dominant species on logs, (3) relationships between log properties and wood decay types, and (4) mycorrhizal infection of seedlings on CWD and soil. Based on the above, I discussed about the effects of wood decay types on seedling densities via log properties and mycorrhizal infection.

## 2. Materials and methods

### 2.1. Study area and background

The study site was located in Higashiyamato Park (35°45′N, 139°26′E; 114–122 m a.s.l.), 40 km west of Tokyo, Japan. The mean annual temperature at the nearest meteorological station in Tokorozawa (35°46′N, 139°25′E; 119 m a.s.l.) from 1979 to 2000 was 14.1 °C. The mean monthly temperature ranged from 3.6 °C in January to 25.5 °C in August. The mean annual precipitation was 1443.9 mm, and there was rarely snow in winter (Japan Meteorological Agency, 2011). The park area of 184 ha was surrounded by residential district. The forest was an abandoned coppice of *Quercus serrata* and *P. densiflora* that had been thinned on a 20–25 year cycle until the late 1970s. The park was established in 1979 and the most recent clear cut of this area (excluding *P. densiflora*) took place from 1982 to 1986. There was widespread mortality in the dominant *P. densiflora* canopy as a result of the pine wilt disease, which began in the 1980s and is still continuing. These tree deaths provided abundant quantities of woody substrate on the forest floor (Kato and Hayashi, 2006). Presently, the canopy is dominated by *P. densiflora* and *Q. serrata* (Table 1), and the understory is dominated by the herb *Pertya scandens*, the grass *Lophatherum gracile*, the dwarf bamboo *Pleioblastus chino*, and lianas such as *Parthenocissus tricuspidata* and *Trachelospermum asiaticum*.

**Table 1**
Community composition in basal area (BA) and stem number for all woody species ⩾1 cm diameter in study plots.

| Species | BA ($m^2$ $ha^{-1}$) | Number $ha^{-1}$ |
|---|---|---|
| *Pinus densiflora* | 9.36 ± 3.52 | 80 ± 31 |
| *Quercus serrata* | 9.24 ± 2.57 | 270 ± 67 |
| *Carpinus tschonoskii* | 1.57 ± 0.84 | 40 ± 17 |
| *Prunus jamasakura* | 1.29 ± 0.80 | 60 ± 23 |
| *Clethra barbinervis* | 0.99 ± 0.37 | 390 ± 176 |
| *Carpinus laxiflora* | 0.92 ± 0.46 | 120 ± 62 |
| *Prunus buergeriana* | 0.78 ± 0.46 | 50 ± 32 |
| *Vaccinium oldhamii* | 0.71 ± 0.75 | 40 ± 42 |
| *Styrax japonica* | 0.64 ± 0.23 | 130 ± 42 |
| *Aphananthe aspera* | 0.60 ± 0.41 | 30 ± 16 |
| *Ilex macropoda* | 0.50 ± 0.25 | 170 ± 85 |
| *Prunus grayana* | 0.45 ± 0.30 | 40 ± 23 |
| *Mallotus japonicus* | 0.34 ± 0.24 | 30 ± 22 |
| *Swida controversa* | 0.32 ± 0.34 | 10 ± 11 |
| *Lyonia ovalifolia* var. *elliptica* | 0.25 ± 0.17 | 210 ± 168 |
| *Magnolia praecocissima* | 0.15 ± 0.16 | 10 ± 11 |
| *Fraxinus sieboldiana* | 0.07 ± 0.07 | 10 ± 11 |
| *Pourthiaea villosa* var. *laevis* | 0.03 ± 0.03 | 30 ± 32 |
| *Rhus trichocarpa* | 0.02 ± 0.01 | 50 ± 32 |

Mean ± S.E. ($n$ = 10 plot).

### 2.2. Field measurements

Ten 10 × 10 m plots were randomly selected within an approximately 1 ha tract on a gentle north slope at the study site. The number and basal area of adult trees (diameter at breast height >1 cm) was recorded at each site. Substrate patches on the forest floor were categorized as either *P. densiflora* CWD (fallen logs and rotten stumps >10 cm diameter) or soil. Diameters of logs and stumps ranged from 10 to 47 cm and 25 to 60 cm, respectively. In the study area, few CWD were derived from broad leaved trees. Logs were classified into five subcategories according to decay classes by employing the criterion of Heilmann-Clausen (2001) after minor modifications as follows: (I) wood hard, penetrable with a knife to only a few mm, bark and twigs (diameter <1 cm) intact; (II) wood rather hard, penetrable with a knife to less than 1 cm, bark and twigs begin to shed away, branches (diameter 1–4 cm) intact; (III) wood distinctly softened, penetrable with a knife to approximately 1–4 cm, bark and branches partially lost, original log circumference intact; (IV) wood considerably decayed, penetrable with a knife to approximately 5–10 cm, bark lost in most places, original log circumference begins to disintegrate; (V) wood disintegrating either to a very soft crumbly texture or is flaky and fragile, penetrable with a knife to more than 10 cm, original log circumference barely recognizable or not discernable. To eliminate within-stem variation in decay stages (Pyle and Brown, 1999), a stem section was selected for each CWD (ca. 2 m along the stem) where decay stage is uniform. The projected areas of all substrates in each plot were estimated as the ground area directly covered by each substrate.

Physicochemical properties (environmental variables) for each log in decay class IV were measured from June to July 2009. Presence or absence of certain decay type in a log was recorded as binary data for sapwood and heartwood separately, regardless of wood mass occupied by certain decay type. In this study, decay types were classified according to the macroscopic criterion of Araya (1993). Brown-rot is reddish-brown and easily breakable into cubical fragments; white-rot is whitish and bleached (yellowish- or grayish-white) and breakable into fibrous fragments; and soft-rot is dull-gray to brown with a mud-like surface. Soil contact