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The geographical gradient of pine log decomposition in Japan

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ABSTRACT

The decay process of coarse woody debris (CWD) is crucial for biodiversity in forest ecosystems. Wood decay types, traditionally categorized into white, brown, and soft rots, are the consequence of fungal decay activities and strongly structure the communities inhabiting CWD. It is important to evaluate the occurrence patterns of the decay types along a geographical range to understand forest biodiversity in wide scale. I examined the effects of environmental variables on the occurrence of wood decay types in pine logs in 30 sites covering a latitudinal gradient in Japan, including sites damaged by pine wilt disease (PWD) in recent decades. Among the wood decay types, the frequency of brown rot was negatively correlated with latitudinal gradient and that of soft rot was positively correlated with mean annual temperature (MAT), suggesting that lignin accumulation during pine log decomposition is more prominent in the warmer lower-latitude areas than in the cooler higher-latitude areas of Japan. In contrast, white rot was negatively correlated with MAT. The effects of precipitation, PWD, log diameter, soil contact, and bark and moss covers on decay type were also apparent. Number of different decay types within a log was negatively correlated with latitude and positively correlated with pesticide. The effects of current vegetation was not detected.

1. Introduction

Decomposing coarse woody debris (CWD) is essential for maintaining forest biodiversity during their decay process. Since different types of CWD provide a variety of habitats for many organisms (Stokland et al., 2012), determining the variation of CWD decomposition is important for understanding forest biodiversity. Fungi are the main agents for CWD decomposition in forest ecosystems (Rayner and Boddy, 1988). The fungal decomposition of wood has been classified into different decay types such as white, brown, and soft rots according to the lignocellulose-decomposition capabilities of various fungal species (Eaton and Hale, 1993). White rot is caused by basidiomycetous and ascomycetous lignin decomposers; wood decomposed by white rot fungi is delignified and becomes whitish with a soft and fibrous texture. Brown rot is caused by basidiomycetous holocellulose-selective decomposers; wood decomposed by brown rot fungi becomes brownish with a fragile cube-shaped texture because relative concentration of lignin increases. Soft rot is caused by ascomycetous microfungi under humid conditions and also relative concentration of lignin increases. Because the decomposition of lignocellulose is a key determinant of the humus formation on the forest floor (Stevenson, 1982), decay types have marked effects on the community structure of detritus-dwelling organisms such as bacteria (Jurgensen et al., 1989; Folman et al., 2008; Hoppe et al., 2014), fungi (Tedersoo et al., 2008; Lindner et al., 2011), invertebrates (Araya, 1993; Cornelius et al., 2002; Wardlaw et al., 2009; Fukasawa et al., 2015), and the plants that grow above the detritus substrates (Bače et al., 2012; Fukasawa, 2012; Fukasawa et al., 2015).

In Japan, a severe dieback of *Pinus densiflora* Sieb. & Zucc. due to pine wilt disease (PWD), which is caused by the induced nematode *Bursaphelenchus xylophilus* vectored by cerambycid beetle *Monochamus alternatus*, started from the 1970s and still continues to date. Consequently, large masses of dead *P. densiflora* logs have accumulated on the forest floor across Japan (Kato and Hayashi, 2006). It was recently reported that the decay type of *P. densiflora* logs is a critical factor determining the community structures of myxomycetes and bryophytes (Fukasawa et al., 2015) and the degree of tree seedling establishments on the logs (Fukasawa, 2012). These results suggest that the local dominance of certain decay types may strongly structure the biodiversity and forest regeneration process after PWD. Because of the high prevalence of damaged *P. densiflora* trees, it is important to evaluate the occurrence patterns of the decay types throughout Japan to understand forest biodiversity and regeneration.

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Since the decay type of CWD is determined by the fungal species that colonize within it, factors affecting the fungal community structure may be indirect but essential drivers of the occurrence of different decay types. Heilmann-Clausen et al. (2014) systematically tested the factors shaping wood decay fungal communities using the data obtained from 26 forest sites in seven European countries and found that climatic factors (such as temperature and precipitation) and forest factors (such as vegetation and forest management regimes) have greater effects, but substrate factors (such as diameter and other properties of the logs) also have substantial effects on fungal communities. In the present study, I examined the effects of these factors on the occurrences of different decay types seen in logs using data from 30 forest sites across Japan. Although Heilmann-Clausen et al. (2014) reported that temperature range (warmest month – coldest month) to be more important for fungal community than MAT, I used MAT as a temperature variable because Tokumasu (2001) suggested that MAT is a necessary climatic variable as well as temperature range for explaining geographical distribution of fungi in Japan, and Berg and McClaugherty (2003) used MAT as a good variable for explaining litter decomposition along geographical gradient. Since decay type properties become apparent in the relatively late stages of wood decomposition, I focused on logs at decay class (DC) IV that is described later.

2. Materials and methods

2.1. Study sites

A total of 30 forest sites were selected along a latitudinal gradient in Japan (Fig. 1, Table 1). Latitude range is from 31.51 (TAN) to 39.49 (KZM), altitude range is from 11 m (KZM) to 1320 m (SDR), MAT range is from 6.3 °C (SDR) to 16.9 °C (TAN), and annual precipitation (AP) range is from 1167 mm (MSH) to 2750 mm (SHB). Farthest two sites (KZM and TAN) are separated from each other about 1200 km. The locations of the sites covered most of the recent distribution of *P. densiflora*, but the current vegetation show a variety of tree species from pure *P. densiflora* stands to *Quercus*-dominated stands, or plantations of commercially grown timber (*Cryptomeria japonica* or *Chamaecyparis obtusa*). Most of the sites experienced PWD during the last few decades, and at some stage underwent management to prevent the spread of PWD (cutting down of infected trees and pesticide treatments).

2.2. Field work

The decay types of sapwood and heartwood of *P. densiflora* logs (diameter >10 cm) were recorded for between 28 and 349 logs in each of the 30 study sites (mean 63.5 logs per site) (Table 1) from 2008 to 2013. All logs were categorized into DC IV according to the five-decay class system (Fukasawa, 2012). Wood in this class is considerably decayed, penetrable with a knife to approximately 5–10 cm. The original log circumference begins to disintegrate. The heartwood of each log was exposed using a hand axe. Presence or absence of certain decay types in a log were separately recorded as binary data for sapwood and heartwood, regardless of wood mass occupied by certain decay types. 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 greyish-white) and breakable into fibrous fragments, and soft rot is dull-grey to brown with a mud-like surface. Frequency of each decay type at each site was calculated as the percentage of the logs displaying a certain decay type. Numbers of different decay types were counted for sapwood and heartwood in each log. For example, if only white rot was observed in sapwood of a log, the number of decay type of sapwood of this log becomes one. Thus the decay type number could become one (simple decay type) to three (all decay types, i.e., white, brown, and soft rots). Log diameter, soil contact, bark cover, and moss cover were recorded for each log. Information about the presence or absence of PWD damage and pesticide treatment at each site were obtained by forest management office or the vestiges such as pesticide bottles on the forest floor and plastic sheets covering wood piles. Cut down treatment by man was recorded if the logs had smooth cut surfaces that is obviously distinguished from that of naturally fallen logs.

2.3. Data analysis

The effects of environmental variables on the occurrences of decay types in the logs were tested by a generalized linear mixed model (GLMM) using glmmML package of R 3.1.2 (R development core team, 2014). Latitude, MAT, AP, dominant tree genera, PWD damage, cut down by man, pesticide treatments, and log diameter, soil contact, bark cover, and moss cover were set as fixed effect variables for explaining decay type occurrences (Table 2). Site was set as random effect. Error structures were set as Binomial when the occurrence of each decay type was a dependent variable, or as Poisson when the number of decay types was a dependent variable. Spearman's rank correlation coefficients were calculated to show the correlations between environmental variables.

3. Results

3.1. Correlations among variables

Spearman's rank correlation coefficients between variables are shown in Table 3. Latitude correlated with the largest numbers (six) of variables; MAT, *Pinus*, PWD, cut down, bark cover, and moss cover correlated with four variables; pesticide treatment correlated with three variables; *Quercus* correlated with two variables; and AP correlated with only one variable (latitude). The strongest positive correlation was found between MAT and PWD, reflecting that the pine stands in the warmer sites have been damaged by PWD. The positive correlation between cut down and pesticide was also strong, reflecting that trees that are cut down are often treated with pesticide. The strongest negative correlation was found between *Pinus* and *Quercus* dominations. *Pinus* domination also has strong negative correlations with MAT and PWD. These results reflect that the vegetation in the forests most severely damaged by PWD, particularly in the warmer areas, changed from predominantly pine to oak.

3.2. Decay type

The frequencies (%) of the decay types observed in the sapwood and the heartwood of pine logs at each study site are shown in Table 4. White rot was seen frequently, particularly in the sapwood than in the heartwood (but not in IWD, RIF, and KGM). All sites showed the presence of white rot, and all the logs found at two of the sites (AOB and OHY) had white rot. The frequencies of brown rot and soft rot were generally lower than that of white rot and were more varied among the sites; their maximum frequencies were 76% (in the sapwood at CHT and OHY) and 74% (in the sapwood at TKZ), respectively. There were some sites with no brown or soft rot in the sapwood and the heartwood. A variety of percentages of the logs contained non-decayed, sound heartwood depending on sites. Average number of different decay types per log was 1.2–1.8 in sapwood and 0.7–1.3 in heartwood.

The GLMM results are shown in Table 5. Latitude was negatively correlated with brown rot both in the sapwood and in the