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Calcium concentration in leaf litter alters the community composition of soil invertebrates in warm-temperate forests

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A B S T R A C T

Many studies have shown the effects of aboveground plant species on soil organisms due to differences in litter quality. However, the calcium concentration in soil has received less attention as a controlling factor of soil invertebrate communities, even though it is an essential element for many animals, especially crustaceans. Litter of Japanese cedar (*Cryptomeria japonica*) plantations, which account for 19% of the forested area in Japan, has a higher calcium concentration compared to other taxa such as broad-leaved trees. We predicted that *C. japonica* plantations affect soil invertebrates by altering calcium availability. We compared soil properties including exchangeable calcium concentration and soil invertebrate communities between *C. japonica* plantations and natural broad-leaved forests. Exchangeable calcium was significantly higher in soil from cedar plantations than in that from broad-leaved forests. The invertebrate community composition differed between the two forest types and was best explained by the exchangeable calcium concentration. In particular, two major taxa of soil crustaceans (Talitridae and *Ligidium japonicum*) were found only in cedar plantations. Our results suggest that calcium concentrations in soil are altered in *C. japonica* plantations and that this affects soil invertebrate communities.

Introduction

Soil organisms can be affected by differences in aboveground vegetation (Bardgett and Wardle 2010), often driven by the quality of the litter types (Swift et al. 1979; Berg and McClaugherty 2003). Differences in litter quality among plant species can influence the chemical properties of soil and act as determinants of the community structure of soil invertebrates (Widden and Hsu 1987; Wardle et al. 2006). Because calcium is a major structural component of the proteins that comprise animals, ambient calcium concentrations are strongly linked to animal densities in calcium poor environment (Alstad et al. 1999; Hessen et al. 2000; Ohta et al. 2014). Similarly, soil calcium concentrations can have an important influence on soil invertebrate communities (Springett and Syers 1984). For example, the abundance of some soil invertebrates increase with available soil calcium concentration (Hotopp 2002; Reich et al. 2005; Skeldon et al. 2007).

Global patterns of soil calcium concentration are governed by geological change, acid deposition and annual precipitation (Potter and Conkling 2012; Binkley and Fisher 2013). For example, low rainfall areas (central North America) tend to have greater soil calcium than what is found in the humid Eastern United States (Potter and Conkling 2012). Calcium availability and cycling at the regional scale are governed by numerous factors including forest vegetation dynamics, atmospheric deposition, soil mineral weathering, and losses due to leaching (Likens et al. 1998; McLaughlin and Wimmer 1999; Dijkstra and Smits 2002). However, much research over the last half century has focused on the leaching of calcium due to acid deposition (Likens et al. 1996; Driscoll et al. 2001), with much less emphasis on other factors, such as changes in forest vegetation, even though the calcium concentration in leaf litter varies greatly among tree species.

In this study, we focused on Japanese cedar (*Cryptomeria japonica*, Cupressaceae) because its leaf litter contains ~3% calcium (Xue and Luo 2002; Baba et al. 2004), more than three times the amount in many other taxa, such as fir (*Abies* spp.) and many broad-leaved trees (Kiilsgaard et al. 1987; Reich et al. 2005; Ohta et al. 2014).

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Japanese cedar plantations cover 12% of the total land area and 19% of the forested area in Japan (Forestry Agency 2011). Litter of members of the Cupressaceae family has a higher concentration of calcium compared with other plant families (Kiilsgaard et al. 1987; Ohta et al. 2014). Because soil organic matter in forests is derived mainly from plant litter, the chemical properties of litter affect soil chemical properties (Reich et al. 2005). Indeed, the soil in Japanese cedar plantations has a calcium content that is three to four times higher than that in evergreen broad-leaved forests in some parts of Japan (Tsutsumi 1987; Ohta et al. 2014). Ohta et al. (2014) showed that the calcium concentration in soil and streams, and the density and survival of dominant aquatic crustaceans, were significantly higher in *C. japonica* plantations compared with evergreen broad-leaved forests. However, Ohta et al. (2014) did not assess the effects of forest vegetation on soil animal community through alteration of calcium availability. Soil crustaceans are frequently dominant decomposers in soil systems (O'Hanlon and Bolger 1999), and contain large amount of calcium in their body (Greenaway 1985). Terrestrial crustaceans mainly acquire calcium from their food (e.g. leaf litter) and soil water. Therefore, we anticipate that the calcium concentration in litter affects the community structure of soil organisms in calcium-poor environment.

Addition of inorganic calcium often increases soil pH (Likens et al. 1996; Driscoll et al. 2001; Warby et al. 2009), and therefore, higher calcium concentrations in soil due to differences in forest vegetation are also likely to increase soil pH (Reich et al. 2005). Alteration of soil pH also causes changes in the abundance of soil invertebrates (Hågvar and Abrahamsen 1990; Myrold 1990; Kaneko and Kofuji 2000). Therefore, plantations of *C. japonica* may affect the community structure of soil invertebrates via increased soil pH.

We examined the effect of Japanese cedar (*C. japonica*) plantations on the community structure of soil invertebrates, particularly the density of crustaceans. We conducted field surveys in six plots that differed in surrounding forest vegetation. We predicted (1) that the calcium concentration and soil pH would be higher in *C. japonica* plantations compared to evergreen broad-leaved forests, and (2) that crustacean density would be higher in *C. japonica* plantations than in evergreen broad-leaved forests.

Methods

Study area

We conducted field surveys in the Wakayama Experimental Forest of Hokkaido University (33°40′ N, 135°40′ E; 428 ha; annual mean temperature: 15.2 °C) on the Southern Kii Peninsula of Japan. The geological structure in this region consists of sandstone and mudstone formed during the middle Tertiary (Tateishi 1976). Because of the highly acidic soil and high annual rainfall (∼4000 mm), the area is extremely poor in calcium (Kihira et al. 2005). The forest soils are extremely thin, nearly exposing the bedrock. Japanese cedar was planted in much of the area beginning in the 1960s, and remnant natural evergreen broad-leaved forests are patchy.

We established a sampling plot (50 m × 50 m) in each of six different catchments of the Wakayama Experimental Forest. The plots were located on relatively flat forest floors and separated by 0.2–1.5 km. Three of the six catchments were mostly covered by evergreen broad-leaved forests 'evergreen', and the other three were covered by Japanese cedar plantations 'cedar'. Forests in the 'evergreen' plots were dominated by *Quercus acuta*, *Quercus myrsinifolia*, *Quercus sessilifolia*, *Neolitsea aciculata*, *Eurya japonica*, and *Machilus thunbergii* (Ohta et al. 2014). The *C. japonica* trees in the 'cedar' plots were planted 30–82 years prior to this study. Calcium concentration in the litter of *C. japonica* (3.4%) is about three times higher than in the evergreen broad-leaved species (0.8–1.5%) at this study site (Ohta et al. 2014). Carbon, nitrogen, phosphorus, and magnesium concentrations do not differ significantly among the species, whereas potassium is about three times lower in *C. japonica* compared to broad-leaved species (Ohta et al. 2014).

Sampling

On 24 July 2012, we collected five samples at each plot from the litter and soil layers using core samplers (soil layer: 50 mm in diameter and 50 mm in height, litter layer: 113 mm in diameter and 40 mm in height) to measure soil chemical properties and mass of the litter layer. To determine the soil crustacean density, we established five sampling quadrats separated by over 10 m. We collected crustaceans within the sampling quadrats (25 cm × 25 cm) to a depth of 3 cm (including litter and surface soil layers) on 17 May and 21 September 2013. Soil crustaceans were separated from soil by hand-sorting and placed in 99% ethanol. To examine the community structure of ground-dwelling macroinvertebrates, we established two subplots (20 m × 20 m) in each plot. We collected ground-dwelling invertebrates using five pitfall traps (8 cm in diameter and 6 cm in depth) per subplot. We placed the pitfall traps in each subplot ∼2 m apart on 17 May, 19 July, 19 October, and 18 November 2013, and collected them 3 days later. We counted and identified all invertebrates found in the traps at least to the ordinal level following Aoki (1999) and Ueno et al. (1985).

Sample processing

To measure soil nitrate and exchangeable calcium, we shook (160 rev min^{-1}) a 0.5 g (air-dried mass) subsample of each soil sample in 100 ml of 1 M KCl solution for 1 h, filtered the sample through filter paper (No. 5C; Advantec, Tokyo, Japan), and then stored the suspension at −30 °C until analysis. We analyzed the soil extracts for calcium and nitrate concentration per unit air-dried mass using an inductively coupled plasma (ICP) atomic emission spectrometer (ICPE-9000; Shimadzu, Kyoto, Japan) and the absorptiometric method (Sakata 2000). We placed a 5-g (air-dried mass) subsample of each soil sample in 25 ml 1 M KCl and measured the pH using a pH meter (TOA-DKK, HM-30V; TOA Electronics, Tokyo, Japan). We dried soil subsamples in a drying oven at 60 °C for 24 h and then analyzed 50 mg dried soil samples for carbon and nitrogen concentrations per dry mass using a CN analyzer (Sumigraph NC-900; Sumika Chemical Analysis Service, Osaka, Japan). We dried a 1-g fresh subsample at 60 °C for 48 h to calculate the soil water content as the difference in mass before and after desiccation.

Statistical analysis

The soil properties (mass of the litter layer, water content, pH, C:N ratio, exchangeable calcium, total carbon, total nitrogen, and nitrate concentration) were fit to linear mixed models with forest vegetation type as a fixed factor and plot identity as a random factor. The statistical significance of the effect of the fixed factor in each model was evaluated by a likelihood ratio test ($\alpha = 0.05$).

We performed canonical correspondence analysis (CCA) to explore the relationships between the soil invertebrate composition and soil properties. The invertebrate data from the five pitfall traps on all four sampling dates were pooled for each subplot. Before conducting the CCA ordination, the abundance data for each taxon were standardized to unit variance, and the most important explanatory variables from all soil properties were determined by forward stepwise selection based on Akaike's information criteria and Monte Carlo permutation tests. All statistical analyses were