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Increases in soil water content after the mortality of non-native trees in oceanic island forest ecosystems are due to reduced water loss during dry periods

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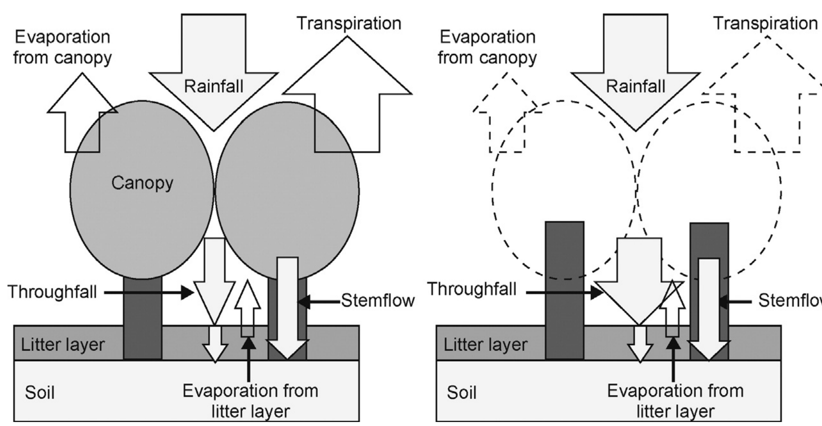
HIGHLIGHTS

- Control of invasive woody species can alter function of forest ecosystems.
- Whether the mortality of an invasive tree alter hydrological processes were tested.
- Surface soil water contents after herbicide treatment of *Casuarina equisetifolia* were measured.
- The mortality of *C. equisetifolia* can decrease site-level water loss through transpiration.
- The control of invasive trees can alter the hydrological processes of a forest ecosystem.

GRAPHICAL ABSTRACT



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ABSTRACT

The control of dominant, non-native trees can alter the water balance of soils in forest ecosystems via hydrological processes, which results in changes in soil water environments. To test this idea, we evaluated the effects of the mortality of an invasive tree, *Casuarina equisetifolia* Forst., on the water content of surface soils on the Ogasawara Islands, subtropical islands in the northwestern Pacific Ocean, using a manipulative herbicide experiment. Temporal changes in volumetric water content of surface soils at 6 cm depth at sites where all trees of *C. equisetifolia* were killed by herbicide were compared with those of adjacent control sites before and after their mortality with consideration of the amount of precipitation. In addition, the rate of decrease in the soil water content during dry periods and the rate of increase in the soil water content during rainfall periods were compared between herbicide and control sites. Soil water content at sites treated with herbicide was significantly higher after treatment than soil water content at control sites during the same period. Differences between initial and minimum values of soil water content at the herbicide sites during the drying events were significantly lower than the corresponding differences in the control quadrats. During rainfall periods, both initial and maximum values of soil water contents in the herbicided quadrats were higher, and differences between the maximum and initial values did not differ between the herbicided and control quadrats. Our results indicated that the

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mortality of non-native trees from forest ecosystems increased water content of surface soils, due primarily to a slower rate of decrease in soil water content during dry periods.

1. Introduction

Invasive, non-native trees often invade and strongly dominate native forests, particularly on islands and some mainland regions (Mueller-Dombois and Fosberg, 1998; Richardson, 1998; Richardson and Rejmánek, 2011). This dominance alters ecosystem functions such as nutrient cycling (Vitousek and Walker, 1989) and hydrological processes (Huddle et al., 2011) through alternations of interactions between organisms and soil. For the purposes of restoration and management of the invaded forest ecosystems, some invasive trees have been controlled in ecosystems (Myers et al., 2000). Although control of exotic species has been the best option in many ecosystems (Courchamp et al., 2003; Genovesi, 2005), it also affects ecosystem functions via biotic interactions and trophic cascades (Zavaleta et al., 2001; Mulder et al., 2009; Ostertag et al., 2009). Understanding how control of exotic species affects ecosystem functions and whether post-establishment changes are reversible is important for restoration and management of the ecosystems (Ostertag et al., 2009; Holsman et al., 2010).

Control of non-native dominant trees can alter ecosystem functions through the loss of large amounts of biomass from the ecosystem. In particular, control can affect hydrological processes. The mortality of dominant trees can change the water balance in the forest ecosystem via changes in water inputs and outputs (e.g., Le Maitre et al., 1999; Andréassian, 2004; Doody et al., 2011; Dovey et al., 2011; Huddle et al., 2011; Dzikiti et al., 2013; He et al., 2014). Water inputs and outputs can be related to changes in forest structure, such as forest canopy and litter accumulation. For example, past studies have found that the mortality of large trees often caused decreases in ecosystem water outputs through losses in transpiration (e.g., Bren et al., 2010; Hawthorne et al., 2013). Furthermore, the loss of tree canopies and accumulated litter associated with control can cause decreases in water interception and evaporation by canopies and litter, both of which may increase soil water inputs (Takahashi et al., 2011). Conversely, the loss of canopies and litter will expose the soil surface, which may increase water output by enhancing evaporation from the soil surface (e.g., Sato et al., 1999; Potts et al., 2008). Overall, these changes may affect soil water conditions, which can affect the establishment of other plants via an increase in water use (e.g., Cordell and Sandquist, 2008; Thaxton et al., 2012).

The fluctuation of soil water conditions through the control of non-native trees can be masked by climatic conditions, especially rainfall and drought. This potential role of rainfall and drought has not been considered by previous studies. To consider the fluctuations derived from rainfall and drought, it is necessary to evaluate how temporal patterns of increase and decrease of soil water content are affected by control of non-native trees using continuous measurements.

Casuarina equisetifolia Forst. (Casuarinaceae) is an invasive woody species, native to Malaysia, southern Asia, Australia, and Oceania, and it has been introduced to various tropical and subtropical regions, including the Caribbean, the Mascarene Islands, the Galapagos, the Hawaiian Islands, and Florida (Weber, 2003). It is strongly dominant in the forests it invades and accumulates large amounts of litter under its dense canopy (Hata et al., 2009). This accumulation prevents the establishment of native trees (Hata et al., 2010) and alters litter decomposition and litter nitrogen release rates (Dutta and Agrawal, 2001; Hata et al., 2012; Rajendran and Devaraj, 2004; Srivastava and Ambasht, 1996). For the purpose of restoration and management of these forest ecosystems, control programs aimed at *C. equisetifolia* have been implemented in Florida (Pernas et al., 2013; Wheeler et al., 2010) and are ongoing on the Ogasawara Islands, located in the northwestern portion of the Pacific Ocean (Government of Japan, 2010).

Water content of surface soils at sites where *C. equisetifolia* trees were experimentally defoliated by herbicides were significantly higher than those at adjacent control sites, which were based on noncontiguous measurements (Hata et al., 2015). This suggests that the soil water balance in these forests shifted positively via changes in water inputs and outputs. These potential inputs and outputs include an increase of throughfall associated with the increased canopy openness caused by the mortality of *C. equisetifolia* trees and a decrease in water loss through transpiration. However, the temporal patterns in water content associated with *C. equisetifolia* mortality, which can result from the above-mentioned processes, are unclear.

In the present study, we addressed three predictions: 1) Soil water content of forests dominated by *C. equisetifolia* increases after its mortality; 2) soil water content after the mortality decreases more slowly during dry periods; 3) soil water content after mortality increases more steeply during rainfall. To test the predictions, we used a manipulative herbicide treatment experiment on a subtropical island in the northwestern Pacific Ocean.

2. Study sites and methods

2.1. Study site

This study was conducted on the island of Nishijima (27°07′10″N, 142°10′00″E; area = 49 ha; highest altitude = 100 m), one of the subtropical Ogasawara Islands in the northwestern Pacific Ocean. The mean values of annual precipitation and temperature between 1969 and 2014 on the largest island (Chichijima) were 25.3 °C and 1269 mm, respectively (Japan Meteorological Agency, Tokyo, Japan). Monthly rainfall during the study period (2012–2013) was highest in May and lowest in July (Fig. 1a). Greater precipitation in October 2012 and September 2013 was due to typhoons. Maximum and minimum temperatures occurred in August and January, respectively (Fig. 1b).

Aerial photographs in 1979 and 2006 showed that the area of vegetation dominated by *C. equisetifolia* increased from 4.6 ha to 17.6 ha (Abe et al., 2011). Abe et al. (2011) suggested that the increase was related to the invasion of *C. equisetifolia* into open forest understory dominated by *Pinus luchuensis* after its die-back caused by pine wilt disease in the early 1980s (Shimizu, 1986). In the 2000s, secondary forests dominated by *C. equisetifolia* were the major vegetation type on Nishijima, while the remaining area was covered by the perennial grass *Zoysia tenuifolia*, a type of secondary vegetation suppressed by feral goat grazing (Abe et al., 2011). Forty-one feral goats were removed in 2002 and 2003, and control was confirmed in 2007 (Government of Japan, 2010), which allowed for a colonization of *C. equisetifolia* into grasslands dominated by *Z. tenuifolia* (Abe et al., 2011). Furthermore, invasive black rats (*Rattus rattus*; density ca. 90 individuals ha^{-1} in 2009; Hashimoto, 2009) had damaged various types of fruiting vegetation (Abe, 2007) by this time. Black rats were controlled with rodenticides between 2007 and 2010, and their population density consequently decreased (Hashimoto, 2009; Kawakami K., unpublished data), which also may have promoted the expansion of *C. equisetifolia*. A program to kill *C. equisetifolia* was implemented in 2010 (Kawakami et al., 2011) and study areas were established to evaluate any effects mortality might have on vegetation recovery processes.

On June 10, 2012, five 10 × 20-m sites were selected in forests dominated by *C. equisetifolia*. At each site, a herbicide treatment was