Invasion of *Leucaena leucocephala* and its Effects on the Native Plant Community in the Ogasawara (Bonin) Islands

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Invasion of *Leucaena leucocephala* and its Effects on the Native Plant Community in the Ogasawara (Bonin) Islands

KEIICHIRO YOSHIDA and SHUICHI OKA

Abstract: To examine the effect of biological invasion by early-successional exotic plant species on the secondary succession of native plant species, we compared secondary forests with and without koa haole invasion, which became established in fields that were abandoned for 55 yr on Chichijima and Haha-jima in the Ogasawara (Bonin) Islands, in the northwestern Pacific. A comparison of the forest structure and the composition of secondary forest showed that the species richness of native plant species was significantly lower, and the basal area of late-successional alien plants (bischofia and Korean mulberry) was significantly larger in secondary forests with koa haole invasion than in those without koa haole invasion. The secondary forests in areas that had been invaded by koa haole had a significantly smaller basal area of native plant species and a greater area of late-successional alien plants in the understory than those in areas that had not been invaded by koa haole. These results suggest that in the Ogasawara Islands, the native species are incapable of replacing dense koa haole thickets directly and that invasion by koa haole promotes invasion and establishment of more aggressive alien plant species. Consequently, the invasion and expansion of koa haole has had a severe effect on the native plant community in the Ogasawara (Bonin) Islands and may alter the secondary succession.

Nomenclature: Bischofia, *Bischofia javanica* Blume; koa haole, *Leucaena leucocephala* (Lam.) de Wit; Korean mulberry, *Morus australis*

Additional index words: Early-successional alien species, late-successional alien species, secondary succession.

INTRODUCTION

Invasion by alien plant species is generally facilitated by anthropogenic and other forms of disturbance (Crawley 1987; Hobbs 1989; Merlin and Juvik 1993) and may give early-successional species greater opportunities to invade new ranges (Ramakrishnan and Vitousek 1989). With no deliberate human intervention, secondary succession related to these alien plant species would proceed.

Attempts to demonstrate the effects of early-successional alien plant species on succession have produced mixed results. Some studies have shown that when alien plant species invade early in succession they are replaced by native plant species, as natural succession proceeds, and they eventually become extinct (e.g., Craig 1993; Franklin et al. 1999; Manner et al. 1985; Yoshida and Oka 2001). In these studies, early-successional alien species did not affect the plant communities seriously. Other studies suggest that the early-successional alien plant species can alter primary and secondary succession (e.g., Myster and Pickett 1992; Vitousek and Walker 1989; Walker and Vitousek 1991) because initial differences in the dominant colonizing species may in turn lead to differences in recruitment under their canopies (Mesquita et al. 2001). However, in these cases, because it is often difficult to know what secondary succession was like before the invasion occurred, it has been difficult to determine how the early-successional alien species have altered secondary succession.

Differences in disturbance history can be implicated in determining secondary succession. Because alien plant invasion is often associated with disturbance (Hobbs and Huenneke 1992), and disturbance alone may lead to changes in community composition and dynamics (Pickett and White 1985), the role of disturbance is
a major confounding factor in the study of the effects of alien plant species on succession (Meiners et al. 2002). Therefore, detecting the effects of early-successional alien plant species on secondary succession requires that vegetation with similar disturbance histories be compared.

In 1944, almost all the agricultural fields on the Ogasawara (Bonin) Islands in the northwestern Pacific were abandoned, and secondary forests have subsequently developed in these abandoned fields. Some of the abandoned fields were invaded by koa haole (Leucaena leucocephala), an alien plant species, whereas neighboring abandoned fields were not. A comparison of these two types of secondary forest provides a unique opportunity to test the role of early-successional alien species in determining secondary succession under relatively equivalent abiotic conditions and disturbance histories.

In this study, we compared the structure and composition of the secondary forests that have developed on the abandoned fields in the Ogasawara Islands to examine the effects of koa haole invasion early in succession on secondary succession after abandonment. The analyses were used to investigate whether the structure and composition of secondary forests with koa haole invasion differed from those of secondary forests without koa haole invasion and whether koa haole invasion affected the regeneration of native plant species.

**STUDY SITES AND METHODS**

Field research was conducted in 1999 and 2000 on Haha-jima and Chichi-jima, which are the two biggest Ogasawara Islands and are located 1,000 ~ 1,300 km south of Tokyo (Figure 1). These islands form an oceanic archipelago that originated from early Tertiary volcanic activity in the Izu–Ogasawara–Mariana Arc. The climate is maritime and subtropical. The mean annual temperature (1970 to 1999) is 23°C, and the mean annual precipitation (1970 to 1999) is 1,234.9 mm in Chichi-jima (Oka et al. 2001). The native vegetation of Chichi-jima can be subdivided into three major types: *Elaeocarpus–Ardisia* mesic forest, *Distylium–Rhaphiole–Shima* dry forest, and *Distylium–Putteria* dry scrub (Shimizu 1992; Shimizu and Tabata 1991).

The Japanese government established dominion over the Ogasawara Islands in 1876 and began to reclaim the islands (Ogasawara Island Agency 1914). Although much of the islands were cultivated until 1944, almost all the land used for farming and housing was abandoned in 1944, when the residents were relocated to mainland Japan.

Koa haole is an invasive leguminous shrub that has become naturalized on many subtropical and tropical Pacific islands where it forms dense thickets in disturbed areas. It was first introduced to the Ogasawara Islands in 1862. Although a few studies have implied that koa haole became naturalized and spread heavily after World War II, little is known about the spatial and temporal dynamics of its distribution. Recently, koa haole has declined on many Pacific Islands (e.g., Decker 1992; Ika-gawa 1993; Mueller-Dombois and Loope 1990; Wester 1992) including the Ogasawara Islands. In the Ogasawara Islands, dense thickets of koa haole have been replaced by late-successional tree species (Yamamura et al. 1999).

After using historical aerial photographs to assess whether koa haole invaded abandoned fields, 24 plots (100 m² each) were established in secondary forests in areas that koa haole invaded during the early-successional stage. We also established 12 plots (100 m² each) in neighboring abandoned fields that were not invaded by koa haole. Four additional plots (100 m² each) were established in natural forests contiguous with the abandoned fields to compare the species composition with both secondary forests. In each plot, the species of every tree (>1.5 m height) was recorded. The diameter at breast height (1.3 m) and tree height were also measured.

![Figure 1. Maps of Haha-jima and Chichi-jima Island in the Ogasawara (Bonin) Islands showing the locations of the study plots.](image-url)
Table 1. Mean of forest structure and composition variables on plots invaded and not invaded by koa haole. Standard deviation in parentheses.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Invaded (n = 24)</th>
<th>Uninvaded (n = 12)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal area (cm²/100m²)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alien</td>
<td>2,080 (953)</td>
<td>1,012 (992)</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>Native</td>
<td>724 (800)</td>
<td>2,767 (1,085)</td>
<td>&lt;0.01*</td>
</tr>
<tr>
<td>Total</td>
<td>2,804 (655)</td>
<td>3,779 (835)</td>
<td>&lt;0.05*</td>
</tr>
<tr>
<td>Species richness</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alien</td>
<td>3.1 (0.9)</td>
<td>2.4 (1.6)</td>
<td>NS*</td>
</tr>
<tr>
<td>Native</td>
<td>5.1 (2.7)</td>
<td>8.8 (3.4)</td>
<td>&lt;0.01*</td>
</tr>
<tr>
<td>Total</td>
<td>8.0 (2.7)</td>
<td>11.1 (3.5)</td>
<td>&lt;0.05*</td>
</tr>
<tr>
<td>Species diversity ($H'$)</td>
<td>1.095 (0.397)</td>
<td>1.313 (0.401)</td>
<td>NS*</td>
</tr>
<tr>
<td>Percentage similarity (%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chichi-jima</td>
<td>9.0 (10.0)</td>
<td>32.4 (11.2)</td>
<td>&lt;0.01*</td>
</tr>
<tr>
<td>Haha-jima 1</td>
<td>12.0 (17.0)</td>
<td>35.7 (25.0)</td>
<td>&lt;0.05*</td>
</tr>
<tr>
<td>Haha-jima 2</td>
<td>10.3 (13.0)</td>
<td>16.6 (11.3)</td>
<td>&lt;0.05*</td>
</tr>
<tr>
<td>Haha-jima 3</td>
<td>9.2 (11.4)</td>
<td>24.0 (15.8)</td>
<td>&lt;0.001*</td>
</tr>
</tbody>
</table>

*a t-test.
*b Mann-Whitney U-test.

To quantify the effect of koa haole invasion on secondary succession, basal area (cm²/100 m²), species richness, species diversity ($H'$), and percentage similarity with each of the natural forest plots (Chichi-jima and Haha-jima 1 to 3) were compared between plots invaded by koa haole (invaded plots) and those that were not (uninvaded plots). To determine the influence of koa haole invasion on the regeneration of native plant species, we also compared the structure and species composition in the understory (1.5 to 3.0 m in height) between invaded and uninvaded plots. For the comparative study, the statistical analyses were performed using t test and Mann–Whitney U tests. All statistical analyses were carried out with the S-PLUS, Version 6.0.3

RESULTS AND DISCUSSION

We found 12 alien and 34 native plant species in the study sites. Only one of the 36 plots established in the abandoned fields was free of alien plant species.

This study showed that the structure and composition of the invaded plots clearly differed from those of the uninvaded plots (Table 1). The total basal area of secondary forest was on average 26% less in plots invaded by koa haole than in uninvaded plots. Invaded plots had a significantly smaller basal area of native plant species than uninvaded plots (t test, P < 0.001). The species richness of native plants was also significantly lower in invaded plots than in uninvaded plots (Mann–Whitney U test, P < 0.01). All percentage similarity indexes with the contiguous natural forests indicated that the species composition was more similar to that of the contiguous natural forests in the uninvaded plots than in the invaded plots. Although there was a negative association between koa haole invasion and the species richness of native species, species diversity did not differ between invaded and uninvaded plots.

Invaded plots had a smaller basal area of native plant species in the understory than in uninvaded plots (Figure 2, Mann–Whitney U test, P < 0.001). The basal area of other alien plant species bischofia (Bischofia javanica) and Korean mulberry (Morus australis) was greater in the forest understory in invaded plots than in uninvaded plots (Mann–Whitney U test, P < 0.05). Bischofia and Korean mulberry are late-successional alien plant species in the Ogasawara Islands and were the main components of the late-successional secondary forests that replaced koa haole scrub in invaded plots. The basal area of koa haole in the forest understory was also greater in invaded plots than in uninvaded plots.

Our comparative study clearly demonstrated that the early-successional alien tree species koa haole has had significant, negative effects on plant communities in the Ogasawara Islands. Koa haole colonized fields immediately after their abandonment in 1944 and then was gradually replaced by late-successional tree species during the last two decades, as secondary succession progressed. In half of the invaded plots, koa haole had disappeared completely by 2000 (F. Ikeda, personal communication). Nevertheless, there were clear differences

3 S-PLUS, Version 6.0, Insightful Corporation, Seattle, WA.
in the structure and composition of secondary forest with and without koa haole invasion; the former had more alien and fewer native plant species than the latter.

This early-successional alien species appears to have an ongoing effect on the species composition of individuals recruited in koa haole scrub. The comparison of the structure and composition of the understory of invaded and uninvaded plots suggested that koa haole invasion early in succession restricted the regeneration of native plant species and promoted the establishment of more aggressive late-successional alien species (bischofia and Korean mulberry). Consequently, the species native to the Ogasawara Islands were incapable of replacing the koa haole scrub established immediately after abandonment, and alternative secondary forests dominated by late-successional alien plant species (bischofia and Korean mulberry) developed at these sites.

A few studies have also reported the replacement of koa haole scrub by other alien plant species. For example, in humid areas on the Hawaiian Islands, Brazilian peppertree (*Schinus terebinthifolius*) asserted dominance after koa haole scrub dieback (Mueller-Dombois 1992). Mueller-Dombois and Fosberg (1998) also suggested that fast-growing alien secondary forest tree species could supplant koa haole scrub in New Caledonia. However, it is unclear whether these invasions were caused by the establishment of koa haole scrub early in succession because of a lack of comparison with forests in areas that were not invaded by koa haole under equivalent abiotic conditions and disturbance. Furthermore, some contrary results, in which native plant species replaced koa haole scrub directly (e.g., Craig 1993; Yoshida and Oka 2001), confound this speculation.

This study found that the neighboring secondary forests without koa haole invasion had fewer late-successional alien species; therefore, the native plant species are not necessarily weaker competitors than the late-successional alien plant species in the abandoned fields of the Ogasawara Islands. Furthermore, the secondary forests dominated by late-successional alien plant species were established only in the abandoned fields invaded by koa haole, and the secondary forests in the abandoned fields without koa haole should approach natural forest as secondary succession proceeds. Such findings indicate that the limitation of the regenerated species in koa haole scrub was of primary importance in determining the characteristics of secondary forests and the degree of invasion by late-successional alien species on abandoned fields in the Ogasawara Islands. These results also suggest that the invasion and expansion of early-successional alien species may have a severe effect on native plant communities by changing secondary-successional pathways.

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**LITERATURE CITED**


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