

ALTERATION OF SECONDARY-SUCCESSIONAL PATHWAYS ON NORTHWESTERN PACIFIC ISLANDS BY THE INVASION OF *LEUCAENA LEUCOCEPHALA*

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Abstract It is commonly believed that plant communities on continental islands are less susceptible to invasion by exotic plant species than are those on oceanic islands, due to their greater native diversity. To test this hypothesis, we compared the successional pathways in abandoned fields invaded by *Leucaena leucocephala* on Haha-jima, an oceanic island, and Miyako-jima, a continental island. Although *L. leucocephala* scrub established on both subtropical islands immediately after agricultural abandonment, there was a significant difference in the secondary-successional pathways. On Haha-jima, the invasion of this alien species altered the secondary-successional pathway irreversibly by restricting the establishment of indigenous species. In contrast, it did not affect the secondary-successional pathway as seriously on Miyako-jima, where indigenous species of fast-growing secondary trees such as *Macaranga tanarius* and *Melanolepis multiglandulosa* replaced dense thickets of *L. leucocephala*. These results provide evidence for the hypothesis that simple communities on oceanic islands are more susceptible to invasion by *L. leucocephala* than diverse communities on continental islands. It is possible that the apparently high ability of *L. leucocephala* to invade Haha-jima is due to the scarcity of indigenous, fast-growing secondary forest species.

Key words: biological invasion, Haha-jima in the Ogasawara Islands, *Leucaena leucocephala*, Miyako-jima in the Ryukyu Islands, secondary succession

1. Introduction

Plant invasion is increasingly recognized as one of the most important subjects in ecology and conservation biology (Pyšek 1995). The biological invasion of alien plant species is a worldwide phenomenon with recognized negative effects on native flora and ecosystems (Vitousek *et al.* 1987; Drake *et al.* 1989). Therefore, to prevent the spread of alien species into unaffected areas, we must not only investigate the pattern and process of biological invasion by alien plant species, but also predict the invasibility of the plant communities.

It is commonly believed that plant communities on continental islands are less susceptible to invasion by exotic plant species than are those on oceanic islands, owing to their greater native diversity (e.g., Vitousek *et al.* 1987; Denslow 2003). Both historical empirical studies and more recent theoretical studies support the predicted negative relationship between diversity and invasibility (Levine and D'Antonio 1999;

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Kennedy *et al.* 2002). However, some ecologists have reported conflicting evidence. For example, Loope and Mueller-Dombois (1989) inferred that taxonomic disharmony or low species number contributed to invasion vulnerability only in a minor way, although they implied that low diversity was a probable cause. Rejmánek (1996) reported similar results. Despite many attempts to describe the relationship between diversity and invasibility, the diversity resistance hypothesis does not sufficiently explain the higher ability of alien plant species to invade oceanic islands.

The islands of Haha-jima and Miyako-jima have similar maritime subtropical climates and generic floristic elements, but obviously different floristic richness; 724 seed plant species are found on Miyako-jima versus only 291 on Haha-jima. *Leucaena leucocephala*, an invasive leguminous tree, was already introduced to both islands. However, a comprehensive assessment of its effects on native plant communities has not been conducted, and its impact may differ depending on plant species richness. Thus, an examination of the impact of *L. leucocephala* on the native plant communities of both islands will provide an opportunity to test the diversity resistance hypothesis.

I reviewed the existing literature on the impact of *L. leucocephala* on the successional progress of abandoned fields on Haha-jima and Miyako-jima. I also compared the effects of invasion on the native plant communities between the two islands by addressing the following two questions: (1) Did *L. leucocephala* invasion change the successional pathway of abandoned fields? If so, how? (2) If its effects differed between the islands, what caused this difference?

2. Study Area

The study areas were Haha-jima in the Ogasawara (Bonin) Islands and Miyako-jima in the Ryukyu Islands (Fig.1). Both islands are located in the subtropical climate zone of the northwestern Pacific. The Ryukyu and Ogasawara archipelagos form a common phytogeographic unit (Ono 1989). Of the 77 woody genera native to the Ogasawara Islands, 90% are shared with the Ryukyu Islands (Shimizu 1989).

Haha-jima (26°08' N, 142°09' E) has an area of 2,080 ha and is the highest subtropical oceanic island (reaching 461 m) in the Ogasawara Islands. The mean annual temperature is about 23.0°C, and the mean annual precipitation is 1276.7 mm at Oomura on Chichi-jima, located 50 km north of Haha-jima (1971–2000, Yoshida *et al.* 2006). In total, 291 indigenous and naturalized plant species occur on Haha-jima (Kobayashi and Ono 1987). Although almost all of the land with moderate topographic relief on Haha-jima was cultivated in 1944, all farmland was abandoned during World War II. In the 64 years since, most of this land has become even-aged secondary forest.

Miyako-jima (24°50' N 125°35' E) is a subtropical continental island in the Ryukyu Islands. The mean annual temperature is about 23.3°C, and the mean annual precipitation is 2019.3 mm at Miyakojima City on Miyako-jima (1971–2000). Many more plant species are found on Miyako-jima (total of 724) than on Haha-jima (Azuma and Kinjo 1981). Secondary forests of various ages are scattered throughout the island (Yoshida and Oka 2001).

Leucaena leucocephala, which is native to Central American savannas, is an invasive leguminous tree that has become naturalized in many subtropical and tropical Pacific islands, where it forms dense thickets in disturbed areas. Recently, late-successional tree species have replaced dense thickets of *L. leucocephala* on both the Ogasawara (Yamamura *et al.* 1999) and Ryukyu Islands (Nakasuga *et al.* 1990), providing an opportunity to assess the effects of *L. leucocephala* on the secondary succession pathway on the two islands.

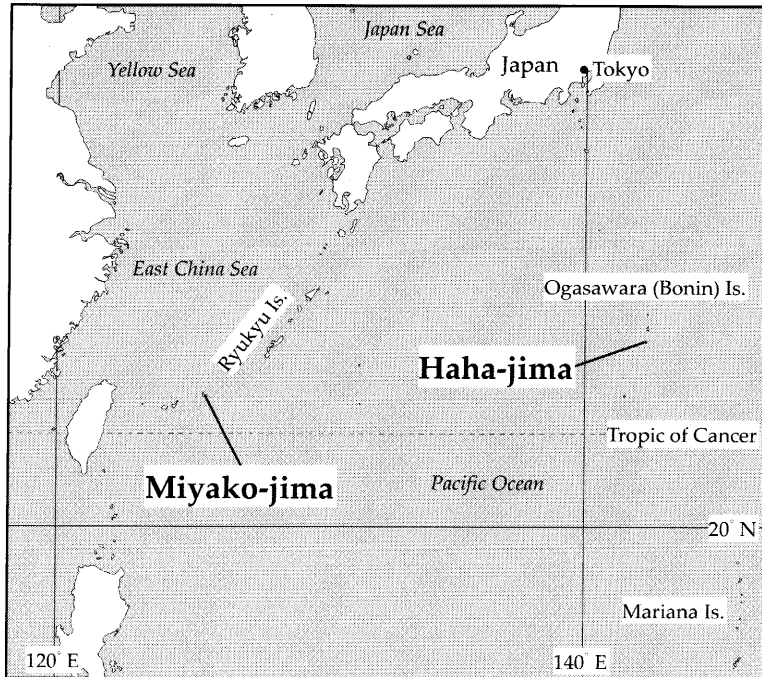


Fig. 1 Locations of Haha-jima and Miyako-jima in the northwestern Pacific.

3. The Effects of *L. leucocephala* Invasion on Secondary Succession.

Haha-jima and Miyako-jima experienced substantially different secondary successional pathways following invasion by *L. leucocephala* (Fig. 2).

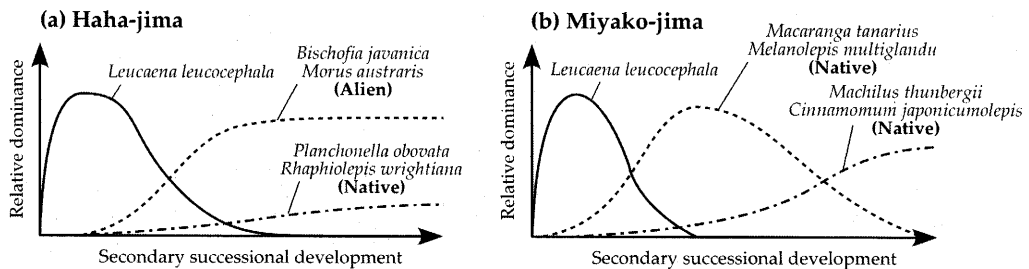


Fig. 2 Schematic of secondary succession patterns after *Leucaena leucocephala* invasion on (a) Haha-jima and (b) Miyako-jima.

On Haha-jima, Yoshida and Oka (2000) demonstrated that late-successional secondary forests in invaded areas differed strikingly in forest structure, composition, and species diversity from those in

unaffected areas. Yoshida and Oka (2004) reported that late-successional alien species such as *Bischofia javanica* and *Morus australis* dominated the former areas, because the dense thicket of *L. leucocephala* restricted the establishment of native successional species and promoted the regeneration of more aggressive alien tree species. In contrast, late-successional secondary forests in uninvaded areas were more similar to the remaining natural forests in terms of forest composition and species diversity (Yoshida and Oka 2000). These results strongly suggest that *L. leucocephala* invasion irreversibly altered the secondary successional pathway.

The change in secondary succession on Haha-jima was caused by multiple invasions (e.g., human disturbance, ungulate grazing, invasions of other alien species), all of which create and exploit new ecological habitats (Loope and Mueller-Dombois 1989). Because *L. leucocephala* formed dense monotypic thickets during early successional stages and outcompeted other species, new successional habitats for the late-successional alien species were created in the secondary successional sequence. The replacement of *L. leucocephala* scrub by multiple invaders has also been reported on a few other Pacific islands. For example, in humid areas of *L. leucocephala* scrub on the Hawaiian Islands, another alien tree, *Schinus terebinthifolius*, became dominant as the scrub died off (Mueller-Dombois 1992). In New Caledonia, if fire is suppressed in the savanna landscape long enough, fast-growing alien tree species will supplant *L. leucocephala* scrub (Mueller-Dombois and Fosberg 1998). On Haha-jima, because few indigenous species exist to replace *L. leucocephala* scrub, the vacant successional habitats are consequently filled by late-successional alien species (e.g., *B. javanica* and *M. australis*), a process called defective succession (Fig. 2a).

On Miyako-jima, Yoshida and Oka (2001) reported that dense thickets of *L. leucocephala* were replaced directly by native species of fast-growing secondary trees (*Macaranga tanarius* and *Melanolepis multiglandulosa*) in the early successional stage, because these species grow quickly and hence are not constrained in their development beneath mature *L. leucocephala* canopy. Secondary succession probably led to late-successional secondary forests that replaced *L. leucocephala* scrub; these forests are similar to mature secondary forests with primary-forest species (*Machilus thunbergii* and *Cinnamomum japonicum*). Originally, the fast-growing secondary-forest species *M. tanarius* and *M. multiglandulosa* were also the early invaders of abandoned fields on Miyako-jima. Therefore, following the replacement of *L. leucocephala* scrub, indigenous mature secondary forest, made up of primary-forest species such as *M. thunbergii* and *C. japonicum*, could develop through normal succession (Fig. 2b). In other words, *L. leucocephala* scrub that grew following agricultural abandonment ultimately reverted to indigenous mature secondary forest on Miyako-jima (Yoshida and Oka 2001).

On Haha-jima Island, *L. leucocephala* irreversibly altered the secondary successional pathway of abandoned lands by interacting with indigenous tree species. In contrast, its impact on succession was much less serious on Miyako-jima. These results support the hypothesis that species-rich communities on continental islands are less invasible by this alien species than species-poor communities on oceanic islands. It is possible that the high ability of *L. leucocephala* to invade Haha-jima was due to a scarcity of native fast-growing secondary tree species, which would have otherwise replaced *L. leucocephala* scrub.

4. Geographic variation in Secondary Succession Affected by *L. leucocephala* Invasion

The ability of *L. leucocephala* to invade also depends on the existence of indigenous tree species that play an important role in secondary succession (e.g., *M. tanarius* and *M. multiglandulosa* on Miyako-jima).

Consequently, there is a negative relationship between species diversity and invasibility. Paradoxically, this suggests that the ability of *L. leucocephala* to invade species-poor communities is low even on oceanic islands with fast-growing and aggressive indigenous flora. In fact, on the tropical oceanic Mariana Islands, pure stands of *L. leucocephala* were replaced by fast-growing secondary-forest species, as on Miyako-jima (Craig 1993; Mueller-Dombois and Fosberg 1998). Considering the impact of invasion on Haha-jima, Miyako-jima, and the Mariana Islands, collectively, these data suggest that the distribution of fast-growing secondary trees has a determinative effect on the pattern of *L. leucocephala* invasion on islands.

Figure 3 shows the distribution of *Macaranga* spp. and *L. leucocephala* throughout subtropical and tropical Pacific islands based on flora lists (Merrill 1923; Kanehira 1933; Brown 1935; Masamune 1942; Hui-Lin 1963; Stone 1970; Fosberg *et al.* 1975; Sohmer and Gustafson 1987; Wagner *et al.* 1990; George *et al.* 1993; Orchard *et al.* 1998), a recent global review (Mueller-Dombois and Fosberg 1998), and other recent studies (Palmer 1988; Thaman 1988, 1992; Merlin 1991; Craig 1992, 1993; Decker 1992; Fosberg 1992; Mueller-Dombois 1992; Wester 1992; Wester *et al.* 1992; Whistler 1992; Drake *et al.* 1996; Meyer and Florence 1996; Fleischmann 1997; Franklin *et al.* 1999; McCoy *et al.* 1999). *Macaranga* spp., including *M. tanarius*, occur widely in southern Asia, Australia, and some tropical Pacific islands (Wagner *et al.* 1990), and are typical fast-growing secondary rainforest species (Mueller-Dombois and Fosberg 1998). The geographic range of *L. leucocephala* on Pacific islands is wider than those of *Macaranga* spp., which in general are limited to humid tropical islands. No *Macaranga* spp. occur on the Ogasawara Islands, the Hawaiian Islands, the Marquesas Islands, or New Caledonia. On these islands, *L. leucocephala* becomes an aggressive invader that affects the successional sequence in particular (e.g., Hawaii, Mueller-Dombois 1992; New Caledonia, Mueller-Dombois and Fosberg 1998; Ogasawara, Yoshida and Oka 2000, 2004). On the other hand, *L. leucocephala* invasion is apparently less serious on subtropical and tropical Pacific islands, where the flora include *Macaranga* spp. (e.g., Mariana, Craig 1992, 1993; Christmas Island, George *et al.* 1993; Ryukyu, Yoshida and Oka 2001). These results imply that the ability of *L. leucocephala* to invade is related to the phytogeographic distribution of fast-growing secondary-forest species on subtropical and tropical Pacific islands.

5. Conclusion

Previous studies exploring *L. leucocephala* invasion on Haha-jima, an oceanic island, and Miyako-jima, a continental island, demonstrated clear differences in the pattern of secondary succession in response to invasion. These studies also implied that increased species diversity has a negative effect on invasibility.

The initial flora and floristic richness can also affect the invasibility of island plant communities in terms of differences in species pools (Richardson and Pyšek 2006), because assemblages with more species are more likely to have members that can survive invasion (Grime 1997; Hooper and Vitousek 1998; Lepš *et al.* 2001). In fact, a biogeographical comparison of the two islands suggested that the high ability of *L. leucocephala* to invade Haha-jima was due to the absence of indigenous, fast-growing secondary-forest species. Therefore, the geographic variation in the impact of *L. leucocephala* invasion on secondary succession on Pacific islands is not due to species diversity itself but rather to the presence/absence of certain indigenous species.

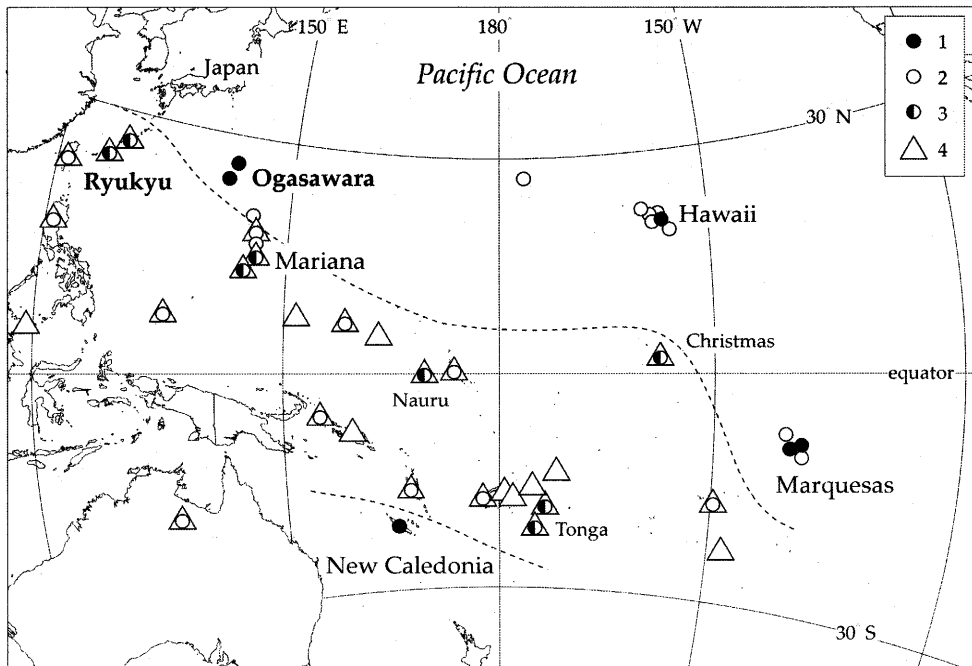


Fig. 3 Preliminary distribution of *Leucaena leucocephala* and *Macaranga* spp.

Leucaena leucocephala became an aggressive invader, and in particular affected the successional sequences outside of the distribution range of *Macaranga* spp.

1: Biological invasion by *L. leucocephala* affected the indigenous island ecosystem. 2: *L. leucocephala* is listed on the island, but its effects are unknown. 3: Although invasion by *L. leucocephala* is observed on the island, it has a reduced effect on the indigenous island ecosystem. 4: *Macaranga* spp. have been reported for the island (the dotted line shows the range of *Macaranga* spp.).

Sources: all Pacific Islands (Mueller-Dombois and Fosberg 1998), Kiribati (Thaman 1988), Nauru and the Gilbert Islands (Thaman 1992), Southern Cook Islands (Merlin 1991), Society Islands (Fosberg 1992), Hawaii Islands (Wester 1992; Sohmer and Gustafson 1987; Wagner *et al.* 1990), Washington Island (Wester *et al.* 1992), Samoa and Tonga (Whistler 1992), Tongatapu Island (Palmer 1988), Vava'u Island Group (Franklin *et al.* 1999), 'Eua Island (Drake *et al.* 1996), Tahiti (Meyer and Florence 1996), Mahe and Silhouette (Fleischmann 1997), Guam (Stone 1970), Northern Mariana Islands (Fosberg *et al.* 1975), Southern Polynesia (Brown 1935), Micronesia (Kanehira 1933), Australia (George *et al.* 1993; Orchard *ed.* 1998), Philippine (Merrill 1923), Taiwan (Hui-Lin 1963).

Acknowledgement

This paper is dedicated to Dr. Shuichi Oka, on his retirement from Tokyo Metropolitan University. I thank Prof. Nobuyuki Hori, Prof. Shuji Iwata, and Prof. Naoki Kachi for their valuable comments. This

paper is based on a doctoral dissertation submitted to the Graduate School of Science, Tokyo Metropolitan University.

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(*: in Japanese, **: in Japanese with English abstract)