PATTERN OF SECONDARY SUCCESSION IN ANTHROPOGENIC HABITATS ON MIYAKO-JIMA ISLAND, THE RYUKYU-ISLANDS, NORTH-WESTERN PACIFIC

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Abstract *Leucaena leucocephala* is an invasive alien plant species in subtropical and tropical Pacific islands. Our previous research showed that biological invasion by this plant species had a serious effect on secondary succession on Haha-jima Island, a subtropical oceanic island. Here, we reconstruct the pattern of secondary succession related to *Leucaena leucocephala* invasion on Miyako-jima Island, another subtropical continental island, to examine the hypothetical negative relationship between diversity and susceptibility to *Leucaena leucocephala* invasion. Although *Leucaena leucocephala* scrub was established immediately following agricultural abandonment, it was replaced within a few decades by a local forest type, dominated by *Macaranga tanarius* and *Melanolepis multiglandulosa*, fast-growing secondary-forest trees found in tropical regions. The dominance of *Machilus thunbergii* and *Cinnamomum japonicum*, which dominated the native primary forests on Miyako-jima Island, gradually increased as secondary succession progressed, and 35-40 years after abandonment, the species composition of the late-successional secondary forests resembled that of the resident mature secondary forest. This pattern of secondary succession shows that the biological invasion of *Leucaena leucocephala* had less affect on Miyako-jima Island than Haha-jima Island. The results in this study therefore provide evidence for the hypothesis that simple communities on oceanic islands are more susceptible than diverse communities on continental islands to biological invasion by *Leucaena leucocephala*.

Key word: biological invasion, diversity-invasibility relationship, *Leucaena leucocephala*, Miyako-jima Island, secondary succession

1. Introduction

Leucaena leucocephala, originally an endemic of Central American savannas, is an invasive alien species that is naturalized mainly in disturbed areas on many subtropical and tropical Pacific Islands (Macdicken *et al.* 1997). In some cases, biological invasion by this alien shrub can very seriously influence the indigenous plant communities. For example, on Haha-jima Island, a subtropical oceanic island that is one of the Ogasawara (Bonin) Islands,

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biological invasion by *Leucaena leucocephala* irreversibly changes the pattern of secondary succession following agricultural abandonment, because it forms dense thickets, and the almost pure stands out-compete most resident plant species (Yoshida and Oka 2000a, b).

It is commonly believed that the plant communities of continental islands are less susceptible than those of oceanic islands to invasion by exotic plant species, due to their higher native diversity. Both historical empirical studies (e.g., Elton 1958) and more recent theoretical studies (e.g., Shigesada *et al.* 1984) consistently support the predicted negative relationship between diversity and invasibility (Levine and D'Antonio 1999). The diverse communities of continental islands are thus expected to minimize the influence of biological invasion by *Leucaena leucocephala* on the pattern of secondary succession, compared to the simple communities of oceanic islands.

In this study, we first attempt to reconstruct the pattern of secondary succession related to *Leucaena leucocephala* invasion on Miyako-jima Island, one of the Ryukyu Islands, in the north-western Pacific, and then test the hypothesis that diverse communities are less susceptible to invasion by exotic species. This information is valuable for biogeographical comparisons of the susceptibility of oceanic and continental islands to invasion, and for understanding more accurately the diversity-invasibility relationship in subtropical island ecosystems.

2. Study Area and Methods

Study Area

Miyako-jima Island (24°43' - 24°56' N, 125°15' - 124°54' E) is located 290 km southwest of Naha City on Okinawa-Honto Island (Fig. 1). The Ryukyu Arc including Miyako-jima Island was probably connected to the Chinese continent via Taiwan, 0.2-0.025 Ma (Kimura 2000). The climate is maritime and subtropical. The mean annual temperate is about 23.1°C, and the mean annual precipitation (1961-1990) is 2033.1 mm at Hirara City on Miyako-jima Island (Japan Meteorological Agency 1996).

The Ryukyu and Ogasawara Islands form a common phytogeographic unit (Ono 1989). Of the 77 woody genera native to the Ogasawara Islands, 90% are also shared with the Ryukyu Islands (Shimizu 1989), and one-third of the seed plants native to the Ryukyu Islands are shared with the Ogasawara Islands (Ono 1989). The three major alien tree species on Haha-jima Island, *Leucaena leucocephala*, *Bischofia javanica*, and *Morus australis*, also occur on the Ryukyu Islands as indigenous (*Bischofia javanica* and *Morus australis*) and alien (*Leucaena leucocephala*) tree species. The regional floristic richness is strikingly higher on Miyako-jima Island than on the Ogasawara Islands (Itow *et al.* 1984; Itow 1988), because of the different geography. There are 724 seed-plant species on the former island (Azuma and Kinjo 1981), and only 291 on the latter islands (Kobayashi and Ono 1987). Therefore, the Ryukyu Islands can be considered a continental island chain that is comparable to the Ogasawara Islands.

Almost the entire area of Miyako-jima Island is utilized for sugarcane plantations. The remaining forests, found only on fault scarps running in a northwest-southeast direction, are mature secondary forests dominated by *Cinnamomum japonicum*, *Ardisia sieboldii*, and

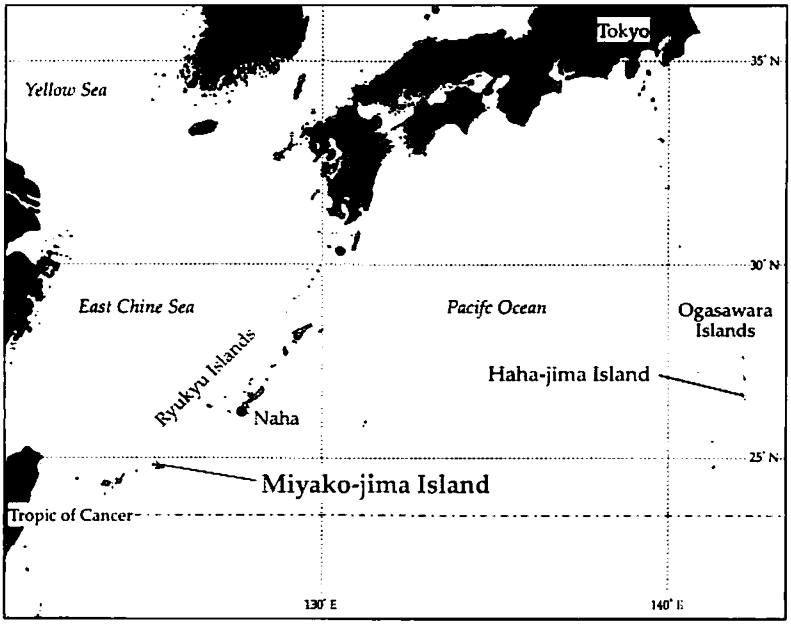

Fig. 1 Location of Miyako-jima Island, north-western Pacific.

Machilus thunbergii. The remaining original forests are a *Macaranga-Bischofia* association (Miyawaki and Suzuki 1976) dominated by *Macaranga tanarius, Bischofia javanica, Machilus thunbergii*, and *Cinnamomum japonicum* (Miyawaki 1989).

Vegetation Sampling

Forest structure and species composition were sampled in 13 quadrats (50-150 m^2), established in 12 abandoned fields and a mature secondary forest (Table 1). In each quadrat, 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. For trees with multiple trunks, the tallest trunk was

Table 1 Some attributes and Importance Values of *Leucaena leucocephala* along a thirty-eight-year chronosequence for each plots in Miyako-jima Island

LOCATION	QUADRAT SIZE (m^2)	ALTITUDE (m)	FOREST AGE (yr)	DENSITY (trees / 100m^2)	FOREST HEIGHT (m)	IMPORTANCE VALUE of *Leucaena leucocephala* (%)
1 Hika	50	91	<5	624	5.0	93.3
2 Sunayama	100	15	6-13	115	6.0	80.2
3 Hukuzato	50	29	6-13	336	7.0	59.6
4 Higashi Nakasone	100	42	14-27	159	6.5	69.4
5 Higashi Nakasone	100	27	14-27	110	7.5	44.9
6 Hirara	100	28	14-27	90	8.0	44.6
7 Ikema	100	20	14-27	78	7.5	31.7
8 Kategari	100	30	28-37	181	7.0	44.7
9 Ikema	100	5	28-37	121	7.0	17.2
10 Yonaha	150	5	28-37	85	8.5	16.6
11 Naganaka	150	66	>38 yr	58	7.5	8.4
12 Higashi Nakasone Soe	100	36	>38 yr	89	6.5	0.0
13 Nohara dake	100	75	mature	115	9.0	0.0

measured. Some tree species with clonal stems were counted as a single individual, but the diameter at breast height was measured for all stems. We conducted our surveys in September and October 2000.

Forest ages were grouped into five classes, corresponding to the time between successive sets of aerial photographs: 0-5 years (n = 1), 6-13 years (n = 3), 14-27 years (n = 3), 28-37 years (n = 3), > 38 years (n = 2). The sources of the historical aerial photographs were the Ryukyu Government (1962, 1:20,000) and The Japan Geographical Survey Institute (1972, 1:10,000; 1986, 1:10,000; 1995, 1:10,000).

Data Analysis

Ordination was used to investigate the chronosequence of secondary forest composition on Miyako-jima Island. Relative basal area, RBA(%), and Importance Value, I.V. (I.V. = (Relative density + Relative Basal Area) / 2), were calculated for every tree species recorded in the 13 plots. The I.V. data sets were subjected to the indirect ordination technique Detrended Correspondence Analysis (DCA, Hill 1979; Hill and Gauch 1980) in order to define the successional sequence. The canopy and lower-story I.V. data of the same species were analyzed separately in DCA ordination, because I.V. depended largely on the canopy individuals, and lower-story individual trees may play a considerable role during secondary succession. PC-ORD ver. 4.1 (McCune and Mefford 1999) was used for the statistical analysis.

3. Pattern of secondary succession on Miyako-jima Island

Patches of *Leucaena leucocephala* scrub were scattered throughout Miyako-jima Island (Fig. 2). According to interpretation of the historical aerial photographs, *Leucaena leucocephala* was established immediately following agricultural abandonment.

The pattern of secondary succession on Miyako-jima Island seemed to show a strong structural and floristic gradient. It was also characterized by a decline in the dominance of *Leucaena leucocephala* (Table 1). The I.V.(%) of *Leucaena leucocephala* was very high during the first five years following abandonment. These values, however, declined gradually as the forest grew older, and *Leucaena leucocephala* had virtually disappeared from secondary forests over twenty-eight years old. This pattern of I.V.(%) suggests that *Leucaena leucocephala* is a typical early-successional species that was replaced by late-successional species during secondary succession on Miyako-jima Island.

Gradient analysis of the secondary-forest composition expanded the above interpretation of the successional pattern. Figure 3 shows the distribution of plots along the first two ordination axes resulting from detrended correspondence analysis (DCA). The eigenvalues for the first two axes were 0.670 and 0.227, respectively. Since the age of the secondary forests increases significantly along Axis 1 (correlation analysis, r = 0.86, $p <$ 0.001), this was interpreted as a secondary-successional sequence. The distribution of plots in the DCA also suggested that the floristic composition of the secondary forests became more similar to that of mature secondary forest (plot 13) as the age of the secondary forests increased along Axis 1.

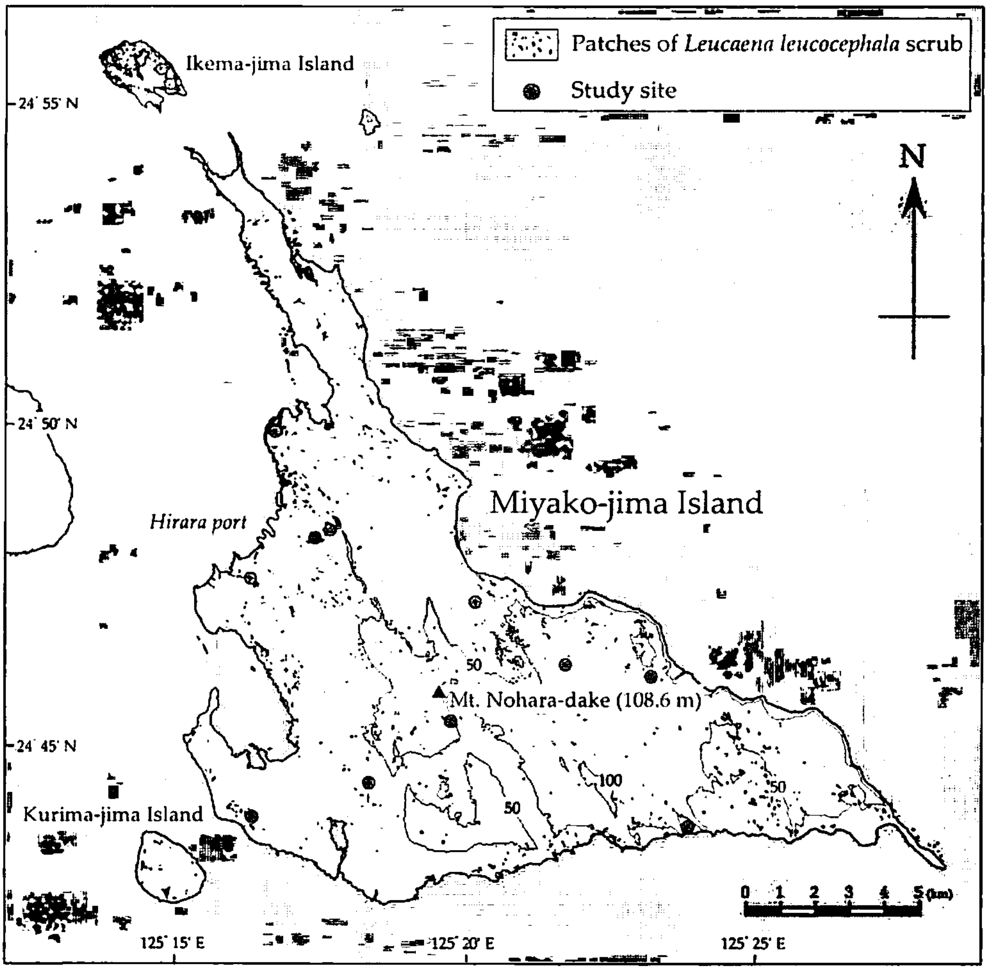

Fig. 2 Location of the study sites in Miyako-jima Island and distribution of the patches of *Leucaena leucocephala* scrubs. The contour lines are 50 m interval.

The size class data for *Leucaena leucocephala* support the interpretation that Axis 1 reflects the secondary successional sequence. The stem-diameter distribution of *Leucaena leucocephala* was examined for five plots, while the age of the forest was determined from the historical aerial photographs (Fig. 4). *Leucaena leucocephala* also displayed the size structure of typical pioneer species, and disappeared gradually as secondary succession progressed. Plot 1 (0 - 5 yr; Axis-1 score = 0.0) showed almost all individuals as in smaller-size classes (< 4 cm DBH), and approximated a reverse-J curve. Plot 3 (6-13 yr; Axis-1 score = 55.2) also had a unimodal size distribution. The frequency of *Leucaena leucocephala* dramatically declined in Plots 8 (14-27 yr; Axis-1 score = 100.9), 10 (28-37 yr; Axis-1 score = 138.5), and 11 (> 38 yr; Axis-1 score = 226.8), and small *Leucaena leucocephala* trees, in particular, were sparse or absent.

The RBA(%) of *Leucaena leucocephala* and two dominant species groups of secondary forests compared to the Axis-1 scores demonstrates the species turnover during the

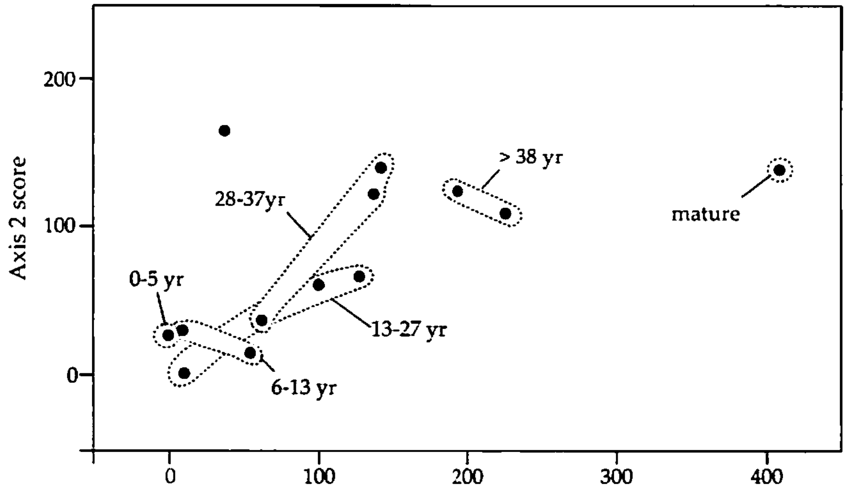

Fig. 3 Detrended Correspondence Analysis (DCA) ordination diagram of the tree species Importance Values within a secondary-successional chronosequence in Miyako-jima island, the Ryukyu Islands. Secondary forests of similar age are enclosed by dotted lines for clarity. Axis 1 is interpreted as a successional gradient, suggesting that floristic composition of the secondary forests become more similar to that of mature forest plots as increasing the forest ages.

secondary-successional sequence on Miyako-jima Island (Fig. 5). The species with the highest RBA(%) in the recently abandoned field was *Leucaena leucocephala*. Its RBA(%) declined sharply as the forest age increased, and the RBA(%) of the resident species group of fast-growing secondary trees (*Macaranga tanarius* and *Melanolepis multiglandulosa*) increased in inverse proportion. These species can be considered as replacing *Leucaena leucocephala* directly. The RBA(%) of the late-successional resident species group (*Machilus thunbergii* and *Cinnamomum japonicum*) gradually increased as secondary succession proceeded. The forest made up of these species ultimately developed into mature secondary forest (Plot 13).

4. Discussion

Secondary succession cannot be monitored directly without long-term field experiments, such as that of Yamamura *et al.* (1999). However, this study does reject the hypothesis that species differences among plots are due mainly to environmental factors, rather than to the age of stands, because topographically or geologically mediated environmental gradients are presumably narrow on Miyako-jima Island. Hence, we can presume that plots surveyed at intervals represent a temporal sequence, and discuss the pattern of secondary succession on Miyako-jima Island, the Ryukyu Islands.

Based on the exploratory analysis of the secondary forest on Miyako-jima Island, we propose the following secondary-successional sequence of tree species replacement: [*Leucaena leucocephala*] → [*Macaranga tanarius*; *Melanolepis multiglandulosa*] →

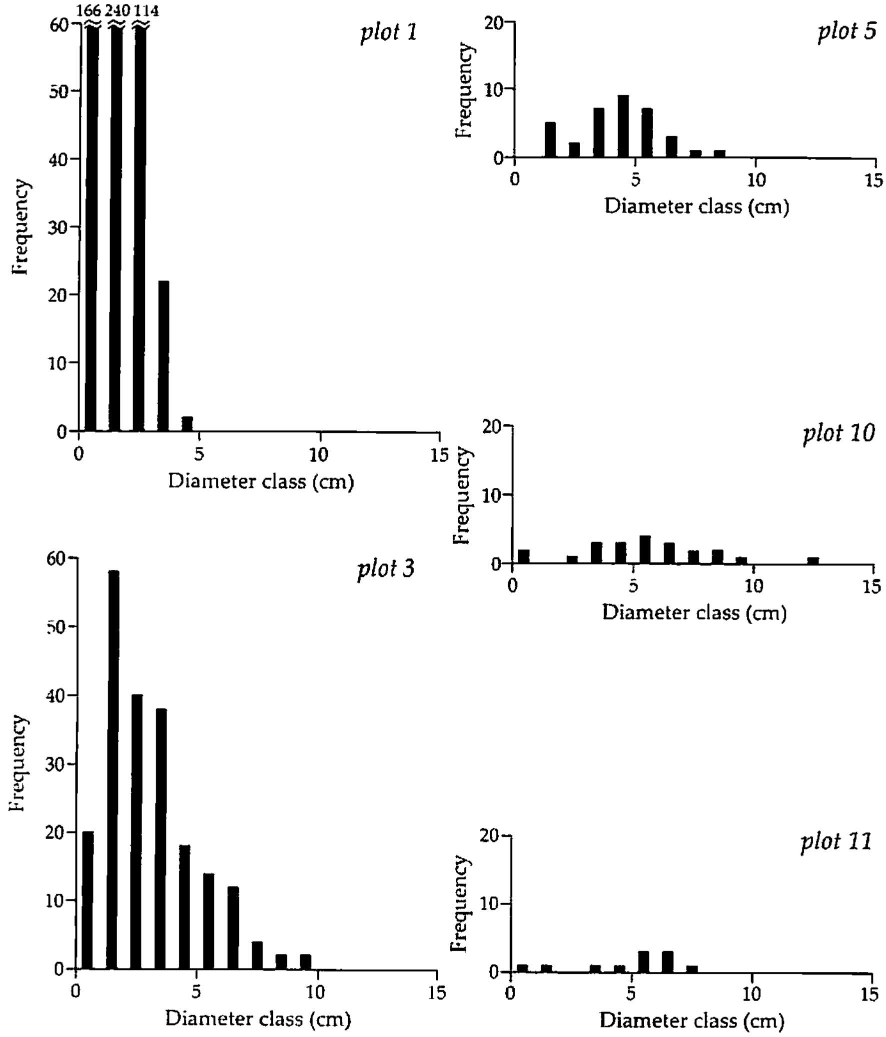

Fig. 4 Size distribution (DBH) of *Leucaena leucocephala* in secondary-successional stages. Number in plot 1 graph indicate frequencies that are incapable of showing. Secondary-successional stage; plot 1: 0-5 yr, plot 3: 6-13 yr, plot 5: 14-27 yr, plot 10: 28-37 yr, plot 11: > 38 yr)

[*Machilus thunbergii*: *Cinnamomum japonicum*]. *Bischofia javanica* and *Morus boninensis*, which replaced *Leucaena leucocephala* scrub on Haha-jima Island (Yoshida and Oka 2000b). are minor species involved in secondary succession on Miyako-jima Island. An exception is Plot 5 (14-27 yr), in which *Bischofia javanica* was one of the dominant species with *Macaranga tanarius* and *Melanolepis multiglandulosa*.

The secondary forest dominated by *Macaranga tanarius* and *Melanolepis multiglandulosa* is very similar to the *Antidesma pentandrum* var. *barbatum-Melanolepis multiglandulosa* communities that have been described as secondary forest on abandoned fields (Miyawaki 1989). These resident, fast-growing, secondary trees replaced *Leucaena leucocephala* scrub more quickly on Miyako-jima Island (20-30 yr).

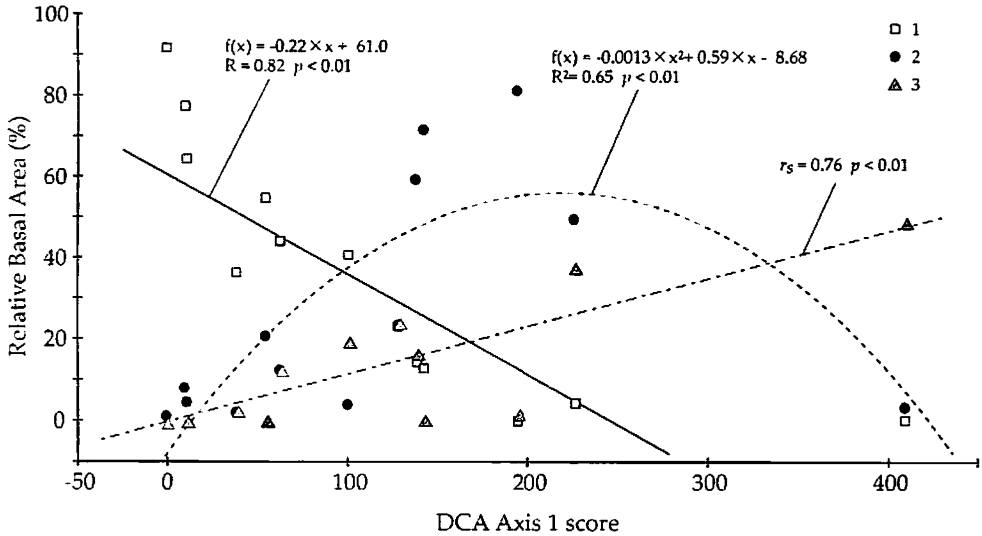

Fig. 5 Relative Basal Area (%) versus DCA Axis 1 score (secondary-successional sequence). *Leucaena leucocephala* decline with increasing Axis 1 score (R = 0.82, $p < 0.01$). The mid-successional species fitted significantly by a second order polynomial ($R^2 = 0.65$, $p < 0.01$). The relative basal area (%) of the late-successional species shows a clear pattern of increase (Spearman rank - correlation coefficient; $rs = 0.76$, $p < 0.01$).

Nakasuga *et al.* (1990) found that many seedlings of late-successional species (e.g., *Cinnamomum japonicum*, *Ardisia sieboldii*, *Elaeocarpus decipiens*) became established on the floor beneath a *Leucaena leucocephala* canopy that was damaged by jumping plant lice (*Heteropsylla cubana*). Their results differ from ours, in that seedlings of the fast-growing secondary-forest species were absent. This difference is probably due to the difference in the vegetation that surrounded the study sites: in the former it was primary or mature secondary forest and in the latter it was cultivated land. That is, the difference in the replacement of species by trees or seedlings may be due to the proximity of primary-forest species, rather than to a difference in the secondary-successional pathway.

The dominance of *Machilus thunbergii* and *Cinnamomum japonicum*, which are the dominant species of the native primary forests on Miyako-jima Island (Miyawaki 1989), gradually increased during secondary succession in this study. As little as 35-40 years after abandonment, the composition of secondary forests resembled that of mature resident forests. In general, in subtropical and tropical regions, the species composition of secondary forests established following abandonment reverts to that of local mature secondary forests within a few decades. For example, the forest composition of 15- to 20-year-old secondary forest reverted to that of late-successional forest in a tropical rain forest in Costa Rica (Reiners *et al.* 1994). Franklin *et al.* (1999) also found that after 30-50 years, secondary tropical rain forest was similar to late-successional forest in terms of forest structure and species diversity on Tonga. Therefore, the pattern of secondary succession seen on Miyako-jima Island, a subtropical continental island, which was less affected by biological invasion by *Leucaena leucocephala*, is more 'normal' than that on Haha-jima Island, a subtropical oceanic island.

5. Conclusions

Biological invasion by *Leucaena leucocephala* did not seriously affect the pattern of secondary succession on Miyako-jima Island. The dense thickets of *Leucaena leucocephala* were replaced directly by resident species of fast-growing secondary trees (*Macaranga tanarius* and *Melanolepis multiglandulosa*), although *Leucaena leucocephala* scrub was established quickly after abandonment. On Miyako-jima Island, agricultural abandonment resulted in reversion, through secondary succession, from *Leucaena leucocephala* scrub to mature secondary forest with the resident tree species.

In conclusion, compared to our previous study of an oceanic island (Yoshida and Oka 2000b), the results of this study support the hypothesis that diverse communities are less susceptible to invasion by exotic species.

Acknowledgement

We wish to thank Prof. Nobuyuki Hori of Tokyo Metropolitan University for his helpful supports and advice. Prof. Shuji Iwata, and Prof. Naoki Kachi provided valuable comments on the manuscript for which we are grateful. We also thank Kumiko Ikura and Fumie Ikeda for their assistance. For members of Laboratory of Environmental Geography, Tokyo Metropolitan University, their valuable discussion is very helpful to this study.

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