

Effects of Past Forest Use on *Ficus* Fruiting Behavior in the Western Lowlands of Yakushima Island

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Introduction

Strangling *Ficus* trees develop a huge crown and produce large amounts of fruit throughout the year. Thus, they can act as “keystone” species in tropical and subtropical forests (Lambert & Marshall 1991; Richards 1996). In the lowlands of Yakushima Island, Japan, located at the southern end of the warm temperate zone, *Ficus superba* var. *japonica* provides fruits for Japanese macaque and various bird species throughout the year (e.g., Hanya et al. 2003), indicating the importance of this species in plant–animal interactions and forest ecosystems. However, it seems that year-round fruiting is more vulnerable in the temperate zone, in which environmental conditions fluctuate seasonally, than in the tropical zone, which has constant high temperatures.

In addition to seasonal changes in environmental conditions, the warm-temperate forest of the western lowlands of Yakushima Island, which is a World Natural Heritage area, experienced human disturbances such as clear-cut logging in the early 1940s (see section 2.1.3.3. for details). Past human impacts can affect the current landscape and tree distribution over a time span of 100 years (Ohtani & Koike 2005). Intensive logging in western Yakushima Island may have also affected ecological functions such as fruit production and the spatial distribution of a keystone *Ficus* species within the forest. Thus, we examined the effects of past logging on *Ficus* fruiting behavior in relation to its distribution and genetic characteristics.

Materials & Methods

The study site of Kawahara was located in the western coastal area of Yakushima Island, southwestern Japan (30°20' N, 130°30' E). The annual mean temperature was 19.8°C, and the monthly mean temperature ranged from 10.6°C in January to 26.2°C in August. This site was covered by secondary warm-temperate broad-leaved forest with dominant species such as *Quercus salicina* (Fagaceae), *Castanopsis sieboldii* (Fagaceae), *Litsea acuminata* (Lauraceae), *Ardisia sieboldii* (Myrsinaceae), and *Distylium racemosum* (Hamamelidaceae). Six *Ficus* species occurred at the study site: two stranglers, *F. superba* var. *japonica* and *F. microcarpa*; a shrub, *F. erecta*; and three vines, *F. nipponica*, *F. thunbergii*, and *F. pumila*. The strangler *F. superba* var. *japonica* occurred frequently in the lowlands of Yakushima Island. The density of the strangler *F. microcarpa* was much lower than that of *F. superba* var. *japonica* at the study site; the island is the northern limit of *F. microcarpa* habitat. Thus, we examined the fruiting phenology of *F. superba* var. *japonica*. Hereafter, “*Ficus* tree” refers to *F. superba* var. *japonica*.

In the Kawahara area, *Ficus* trees inhabited two types of site: sites that were subjected to intensive or clear-cut logging in the early 1940s; and sites that experienced relatively light logging mainly for charcoal production in the 1940s–1950s. Some huge strangler *Ficus* trees were found in the sites used for charcoal

production. In contrast, most *Ficus* trees in the clear-cut sites had relatively small crowns and grew on rocks; these trees seemed to have established after the clear-cut logging.

In total, 74 *Ficus* trees were surveyed using a GPS receiver (Pathfinder Pro XRS, Trimble, Tokyo) and their crown projection area was determined as an index of tree size. Fruiting behavior has been monitored at 3- to 4-week intervals (on average, 26.4 days per interval) since June 2003, and the amount and maturity of fruit is recorded at each census. The amount of fruit was ranked from 0 = no fruit to 8 = vast amount of fruit, indicating the relative fruit abundance within an individual tree. Here, we analyzed data from June 2003 to December 2006.

To examine the relationship between genetic characteristics and fruiting patterns of individual trees, we conducted microsatellite genotyping of the 74 *Ficus* trees monitored. Fresh leaf samples were obtained from each tree between June and August 2004, and DNA was extracted using a DNeasy Plant Mini Kit (QIAGEN). We used six microsatellite primers that were developed for other *Ficus* species: FinsA1, FinsH5, FinsJ10, FinsM5, FM4-70, and FS3-31 (Vignes et al., 2006; Zavodna et al., 2005). The loci were amplified in two multiplex polymerase chain reactions (PCRs), with each containing four and two primer pairs (FinsH5 / FinsM5 / FM4-70 / FS3-31 and FinsA1 / FinsJ10) and 10 ng of template DNA. PCR amplifications were performed using a GeneAmp PCR System 9700 (Applied Biosystems) with: initial denaturation at 95°C for 15 min; 25 cycles of denaturation at 94°C for 30 s, annealing at 57°C for 90 s, and extension at 72°C for 60 s; and a final incubation at 60°C for 30 min and holding at 4°C. PCR products were denatured at 95°C for 3 min and electrophoresed along with the GENESCAN 400-HD ROX size standard on a 3100 Genetic Analyzer using GENESCAN analysis software and GENOTYPER software (Applied Biosystems).

Results & Discussion

Of the 74 *Ficus* trees monitored, four were of relatively small size did not produce any fruits during the study period and so were excluded from the analyses. K-means clustering classified the 70 *Ficus* trees into two groups according to the amount of fruit at each census. The mean amount of fruit for the first group (20 trees) increased periodically in winter (Fig. 1). In contrast the mean amount of fruit for the second group (50 trees) was consistently low, with no apparent seasonal changes. The 20 trees that bore abundant fruit in winter had larger crown projection areas than the remaining 50 trees (U-test, $z = 3.18$, $p = 0.001$; Fig.2). The crown projection area was positively correlated with the fruiting frequency per year ($n = 70$, $r = 0.52$, $p < 0.001$; Fig. 2). This suggests that larger trees have the potential for frequent fruiting within a year and heavy fruiting in winter, which increases their relative contribution to the year-round fruiting and the plant–animal interactions.

The *Ficus* trees in Kawahara were distributed mainly in areas that were not clear-cut logged in the early 1940s, although some relatively small trees inhabited prior intensively logged sites (e.g., Fig. 3, southwestern corner). *Ficus* trees with the two types of fruiting pattern, i.e., heavy winter fruiting or no apparent trend, were randomly dispersed (Fig. 3), indicating no spatial bias in the tree distribution corresponding to the type of fruiting pattern. However, some large *Ficus* trees with heavy winter fruiting were located exclusively in sites that had not been clear-cut in the early 1940s (Fig. 3).

Six microsatellite loci were consistently resolved in the *Ficus* trees. A total of 23 alleles were detected: two for each of FinsJ10, FinsM5, and FS3-31; five for FinsH5; and six for each of FinsA1 and FM4-70. Based on the allele types for these six microsatellite loci, we performed a principal components analysis with respect to fruiting pattern (Fig. 4). The eigenvalues of axes 1 and 2 were 5.27 and 3.82, respectively. *Ficus* trees classified into the two fruiting patterns were scattered randomly in the analysis (Fig. 4), suggesting that the genotypes determined using the six microsatellite loci had no relation to the fruiting behavior and that the fruiting pattern of individual trees was governed by other factors such as variation in solar insolation.

The lack of large *Ficus* trees in the prior clear-cut sites indicated that the sizes and populations of *Ficus* trees are still developing and recovering from human disturbances that occurred approximately 60 years ago. Given their potential for heavy fruiting in winter, large *Ficus* trees can play a much more important role than small trees. However, some large *Ficus* trees growing on rocks or steep slopes fell over, probably as a result of strong wind and their own weight, implying a tree size limitation for *Ficus* tree growing on rocks. Large-sized host trees such as *Persea thunbergii* and *D. racemosum* appear to be required for the development of large strangling *Ficus* trees. Thus, it may take strangling *Ficus* species longer to recover than the general forest structure.

In the lowlands of Yakushima Island, as well as in the coastal areas of southwestern Japan, forests have been exposed to various human disturbances, including conversion to other land uses. Protected areas in lowlands and coastal sites are required to conserve rich ecosystems, including *Ficus*-animal interactions, in the warm temperate zone.

References

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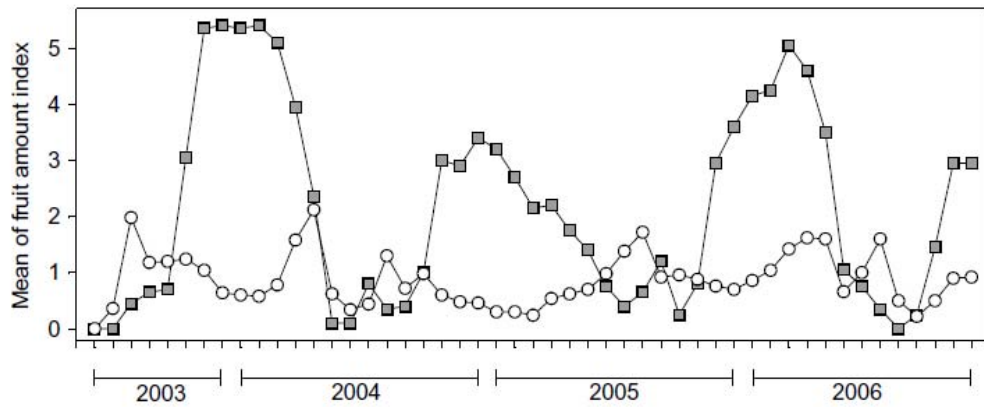


Fig. 1. Time series of the mean amount of fruit for two groups of *Ficus* classified using K-means clustering. One group (gray squares) tended to produce large amounts of fruit in winter; the other group (white circles) had no conspicuous seasonal trend.

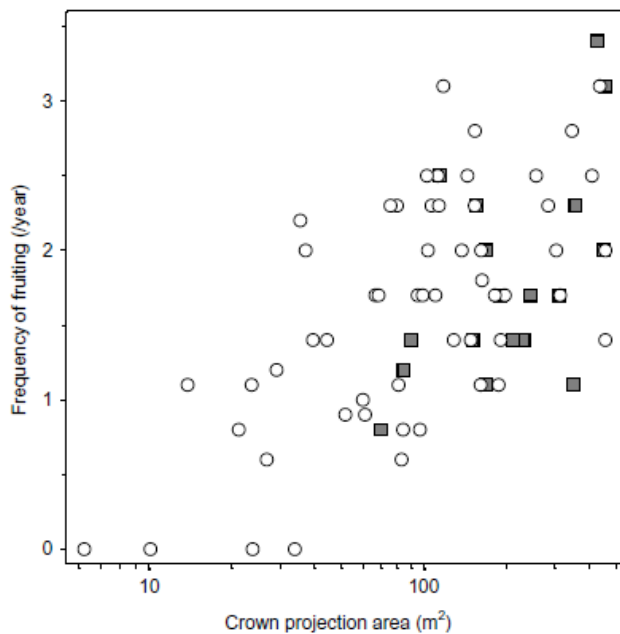


Fig. 2. The relationship between crown projection area and fruiting frequency per year of *Ficus superba* var. *japonica*. A significant positive correlation was detected ($n = 70$, $r = 0.52$, $p < 0.001$); four trees that did not produce fruit during the study period were excluded from the analysis. See Fig. 1 legend for symbols.

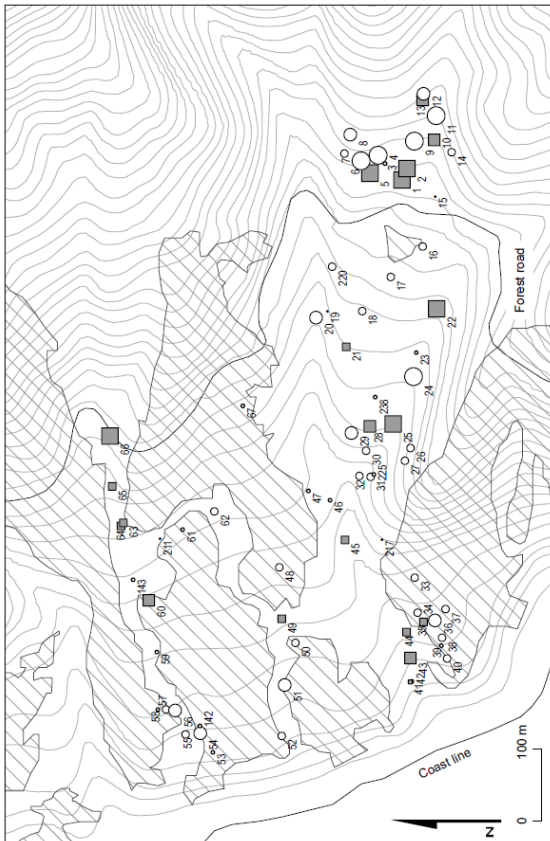


Fig. 3. The locations of *Ficus* trees classified into two groups based on fruiting pattern. See Fig. 1 legend for symbols. Symbol size represents relative tree size in four ranks. Shaded polygons indicate areas that were clear-cut in the early 1940s, derived from aerial photographs taken in 1947.

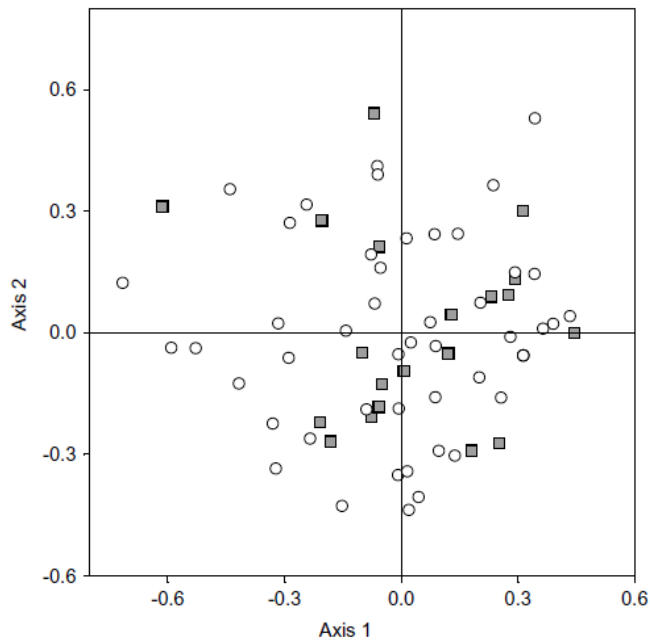


Fig. 4. Principal components analysis of the genotypes of 70 *Ficus* trees characterized using six microsatellite loci. See Fig. 1 legend for symbols.