

JAPANESE OAK WILT AS A NEWLY EMERGED FOREST PEST IN JAPAN: WHY DOES A SYMBIOTIC AMBROSIA FUNGUS KILL HOST TREES?"

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ABSTRACT

Japanese oak wilt (JOW) has been known since the 1930s, but in the last 15 years epidemics have intensified and spread to the island's western coastal areas. The symbiotic ambrosia fungus *Raffaelea quercivora* is the causal agent of oak dieback, and is vectored by *Platypus quercivorus* (Murayama). This is the first example of an ambrosia beetle fungus that kills vigorous trees. Mortality of *Quercus crispula* Blume was approximately 40 percent but much lower for associated species of Fagaceae, even though each species had a similar number of beetle attacks. It is likely that other oaks resistant to the fungus evolved under a stable relationship between the tree, fungus and beetle during a long evolutionary process. *Quercus crispula* was probably not part of this coevolution. This hypothesis was supported by the fact that *P. quercivorus* showed the least preference for *Q. crispula*, yet exhibited highest reproductive success in this species (The index of an increasing rate = ca. 4). On contrary, on the other oaks the index was almost one that guarantees a stable population dynamics for *P. quercivorus*. Therefore, *P. quercivorus* could spread more rapidly in stands with a high composition of *Q. crispula*. Each of individual trees other than *Q. crispula* can be utilized by *P. quercivorus* for several years. On contrary, *P. quercivorus* can reproduce only one year on each *Q. crispula* tree because necrosis of sapwood tissues spread widely after the first-year attack. The relationship among *Q. crispula*—*R. quercivora*—*P. quercivorus* seems evolutionary unstable. JOW seems to be an invasive pest of *Q. crispula*. Concentric patterns of JOW spread also support this hypothesis.

Introduction

Since the late 1980s, Japanese oak wilt (JOW) has been prevalent in Japan (Ito and Yamada 1998). JOW has been recorded since the 1930s, but up to 1980, epidemics lasted for only a few years and were confined to a few areas on the west side of Japan. More recently, epidemics have lasted for more than 15 years, and the area of JOW has been spreading to new localities where JOW has never been recorded in the past. These incidences of oak dieback have tended to spread concentrically from a source population (Kamata et al. 2002), exhibiting a pattern of spread typical of introduced invasive species. *Raffaelea quercivora* was proved to be implicated in JOW by inoculation experiment of the fungus (Ito et al. 1998). The ambrosia beetle, *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae), is a major vector of this fungus (Ito et al. 1998), because (1) affected dead trees are almost always infested by this species; (2) the fungus is found frequently in gallery systems of *P. quercivorus*; and (3) the fungus also occurs inside the beetle's mycangia, in which the fungus is carried to a new host tree.

Ambrosia beetles usually attack weakened or dead trees. The present case in Japan is the first example of an ambrosia fungus carried by an ambrosia beetle that kills vigorous trees. *Platypus quercivorus* can reproduce regardless of host fate following the insect attack. Necrosis has been observed around the gallery systems in sapwood, and has been attributed to *R. quercivora* (Ito and Yamada 1998). The necrosis stops water conductance, and a tree dies when necrosis completely blocks any cross section of the tree (Kuroda and Yamada 1996).

Life history of *P. quercivorus*

Platypus quercivorus is basically univoltine in Japan with an occasional second generation (Sone et al. 1998). Adult emergence of the main overwintering generation was observed from May to September with a peak in early July, and emergence of the second generation has been observed from late August to early December. Dispersal flight of the newly eclosed adults detected by sticky interception traps continued from late June to early December with a peak in July and early August (Esaki et al. 2004). After a male selects a tree for a breeding site, it initially bores a cylindrical entrance hole about 15 mm in extent into the tree. When a female arrives later at the entrance, the male emerges from the entrance and leads the female into the tunnel. After mating at the entrance hole, the male follows the female into the tunnel and she starts to bore a horizontal gallery. A male and female pair reproduce in one galley. On the thorax, a female has a mycangia, in which it carries spores of symbiotic ambrosia fungi. The female lays eggs on the walls of the gallery, inoculating spores of the ambrosia fungi on the wall of the galley. The female grazes on the ambrosia fungi to continue to lay eggs by the end of autumn (mid-November in Ishikawa). The parents were supposed to die before or during the winter because no eggs were found in the spring. The eggs hatch within about a week, and the larvae grazed on the ambrosia fungi covering the walls of the horizontal galley. Larvae pass through five instars. Matured larvae formed pupal cradles vertically and pupated in these cradles. Individuals that could pupate by the autumn (mid-October in Ishikawa) emerge as adults of the second generation. The others overwinter as a larval stage and pupate in the following season.

Preference-performance relationship of *P. quercivorus* among different oak species

Although 45 species among 27 genera in 17 families of woody plants have been recorded as host plants of *P. quercivorus*, woody plants belonging to the Fagaceae are considered as essential hosts of *P. quercivorus* because beetle attack density is significantly higher on trees in this family. There are

many records of *P. quercivorus* outbreaks in stands of evergreen species of Fagaceae in Japan, but few evergreen trees have been killed by this ambrosia beetle fungus even though many entry holes have been found on the trunk surface. In Ishikawa, the mortality of newly attacked *Q. crispula* was ca. 40 percent, but low mortality was observed in associated species of Fagaceae (Kamata et al. 2002). However, the numbers of new entry holes made by this beetle in different species of *Quercus* were similar. Several studies also proved that *Q. crispula* was much more susceptible to this fungus than other sympatric species of Fagaceae.

The reproductive success of *P. quercivorus* differed among the four species of Fagaceae: *Q. crispula* was the most suitable host species for reproduction (mean no. of offspring adults emerged per gallery = ca. 8), while the number was almost two for *Q. serrata*, *Q. acuta*, and *Castanopsis cuspidata* (Kato et al. 2001). *Platypus quercivorus* failed to reproduce in *Q. crispula* and *Q. serrata* trees that had been infested in the previous year. In the second year of this insect attack, adults of *P. quercivorus* avoided the necrosis of sapwood when they tunneled. The advancing necrosis caused by *R. quercivora* was then likely to make the tree less suitable as a substrate for ambrosia fungi and/or for *P. quercivorus*. Hydrolyzable tannin contained in healthy sapwood was converted to ellagic acid and gallic acid by *R. quercivora* tannase (Kasai et al. 2003). Purprogallincarboxylic acid was bio-converted with *R. quercivora* laccase from gallic acid. Hence great amount of ellagic acid (0.05% w/wet weight) and small of gallic acid (0.001% w/wet weight) was contained in discolored necrosis of sapwood (Oana et al. 2003). Adults of *P. quercivorus* avoid these tannic acids in discolored necrosis.

The rate of development of the necrosis is a key to determining tree mortality following *P. quercivorus* attack and reproductive success of this insect in the second year attack and thereafter. Because it was slow by comparison in evergreen species of Fagaceae, these trees are less susceptible to *R. quercivora* than *Q. crispula* and *P. quercivorus* can reproduce on these in the second year attack.

In a stand with a low percentage of *Q. crispula*, *P. quercivorus* showed the least preference for *Q. crispula* (Kamata et al. 2002), although its reproductive success was highest on this species. An inverse relationship was found between the preference of *P. quercivorus* for different tree species and its performance on these species. Its greatest preference was for *Castanopsis sieboldii* (Fagaceae) with 45.6 percent and 67.6 percent of trees attacked in 1999 and 2000, respectively. Because reproductive success of *P. quercivorus* on trees other than *Q. crispula* is low, aerial population density of *P. quercivorus* adults in this stand (L) was lower than in the other stand with a high percentage of *Q. crispula* (H) (H/L=45.8 in 1999, 3.3 in 2000). The percentage mortality of *Q. crispula* was low in this stand and the tree composition of the stand was stable. In the stand with a high percentage of *Q. crispula*, in contrary, infestation spreads out very rapidly on every Fagaceae trees. Tree mortality of newly infested *Q. crispula* was about 40 percent every year, which caused great changes in tree composition.

Thus, the oak *Q. crispula* was preferred least by *P. quercivorus*, but it was the most suitable host for reproduction and was susceptible to the symbiotic ambrosia fungus. The relationship among *Q. crispula*—*R. quercivora*—*P. quercivorus* seems evolutionary unstable. It is likely that other oaks resistant to the fungus evolved under a stable relationship between the tree, fungus and beetle during a long evolutionary process. *Quercus crispula* was probably not part of this coevolution. JOW seems an invasive pest of *Q. crispula*. JOW occurs in the northern regions and high elevation margins of the distribution of *P. quercivorus* and on the southern / low elevation margins of the distribution of *Q. crispula*. JOW epidemic in Japan probably resulted from the warmer climate that occurred from the late 1980s, which made possible the fateful encounter of *P. quercivorus* with *Q. crispula* by allowing the beetle to extend its distribution to more northerly latitudes and higher elevations (Kamata et al. 2002).

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