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History of Pine Wilt Disease in Japan[1]

Y. MAMIYA[2]

Abstract: Pine wilt disease induced by the pinewood nematode, *Bursaphelenchus xylophilus*, is a great threat to pine forests in Japan. The first occurrence of the disease was reported in Nagasaki, Kyushu. During the 1930s the disease occurrence was extended in 12 prefectures, and in the 1940s the disease was found in 34 prefectures. The annual loss of pine trees increased from 30,000 m^3 to 1.2 million m^3 during these two decades. The enormous increase in timber loss in the 1970s resulted in 2.4 million m^3 of annual loss in 1979. The affected area expanded into 45 prefectures of 47 prefectures in Japan. In cool areas the disease differs in epidemiology from that in heavily infested areas in the warm regions. A national project for controlling pine wilt disease lays special emphasis on the healthy pine forests predominating throughout cool areas in northern Japan.

Key words: pinewood nematode, *Bursaphelenchus xylophilus*, pine sawyer, *Monochamus alternatus*, epidemiology.

The pinewood nematode (PWN), *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle, has been discovered so far in the United States, Canada, mainland China, Taiwan, and Japan. In North America, wide distribution of the nematode is not associated with epidemic disease (19). Limited distribution of the nematode in China and Taiwan is related to an intense outbreak of the disease (11). In Japan, a sharp increase in the incidence of the disease has resulted in such damage to the native pines—*Pinus densiflora* Sieb. and Zucc., *P. thunbergii* Parl., and *P. luchuensis* Mayr—that it is a threat to pine forests throughout the country. Its epidemic occurrence in Asia suggests the introduction of the pathogen from outside of Asia.

This paper reviews pine wilt disease in Japan, focusing attention on the present status of this epidemic disease and perspectives for the future.

HISTORICAL REVIEW

An outbreak of pine mortality in Kyushu in the early 1900s was the first reported occurrence of the pine wilt disease in Japan (20). More than 60 years later the primary pathogen of the disease was discovered and an adequate conception of the disease as an epidemic, disseminated by beetles, was adapted for the disease management. During that time, extensive efforts to control the disease employed strategies based on research on the entomological aspects. "Matsukuimushi," which means insects involved in dead pine trees, was the word popularly used to indicate this devastating problem; it is still valid as a legal term.

The pinewood nematode was first described in 1971 as the causal agent of pine wilt disease of native pines in Japan (6). Pine sawyer, *Monochamus alternatus* Hope, was immediately designated as a principal vector of the causal agent (12,14). Quick death of a nematode-infected tree is characteristic of pine wilt disease. Affected pine trees that appear healthy in early summer show a reddish-brown foliage and die by late autumn. This distinguishing characteristic made it easy to diagnose the diseased trees, even before the identity of the causal agent was established. Damage caused by other agents may have been confused with pine wilt disease at a low rate during the years before the nematode was determined to be the causal agent. An increase in loss of pines and extensive spread of the disease, however, can be followed accurately using statistics accumulated by the Forestry Agency of Japanese Government. Since the recognition of PWN as the causal agent, disease diagnosis has always corresponded with nematode infestation.

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[2] Forestry and Forest Products Research Institute, P.O. Box 16, Tsukuba Norin Kenkyu Danchinai, Ibaraki, 305 Japan.

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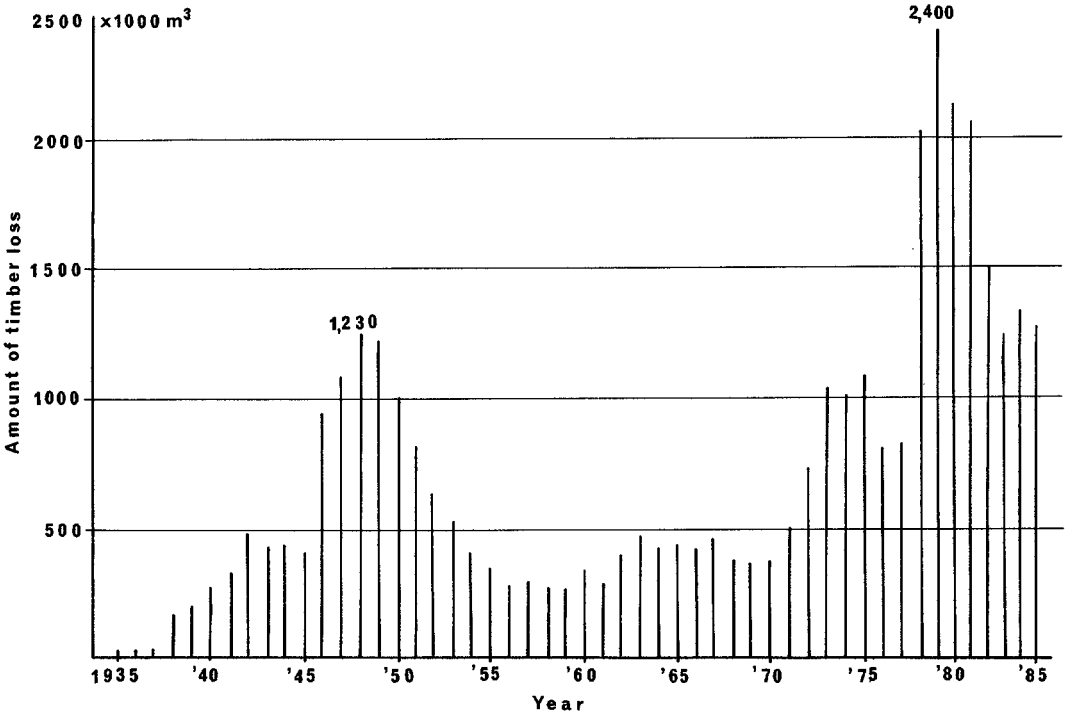

FIG. 1. Annual loss (cubic meters of wood) of pine trees caused by pine wilt disease in Japan. (Forestry Agency, Japan.)

The present status of pine wilt disease in Japan may be traced from the first outbreak in Kyushu.

The 1905 outbreak of pine wilt disease in Nagasaki, Kyushu, was controlled by eradication of dead trees, which prevented the recurrence of the disease in the area. In 1925, the disease was reported in Sasebo, 50 km north of Nagasaki. In this case, no effort was made to control the disease because the affected forests were on military land. Over a period of several years, the disease caused considerable loss of pine trees in the area. Thus an infection center of the disease was established in Kyushu, and disease spread into surrounding areas during the 1930s.

By the late 1930s outlying infections occurred at several locations in Kyushu. In most cases, the disease started in a forest adjacent to a pulp factory. In 1921, pine wilt disease was found in Hyogo prefecture. This outbreak eventually spread extensively along the coast of Seto Inland Sea. During the 1930s and the early 1940s, pine wilt disease spread into 12 prefectures, seven of which were in Kyushu, causing the loss of 2 million m^3 of timber. The annual loss increased from 30,000 m^3 to 400,000 m^3 during those years. In 1948, a loss of 1.2 million m^3 resulted from abandoned attempts at control during World War II (Figs. 1, 2). Infested areas had extended as far as the central part of Honshu and included 34 prefectures. Extensive control efforts, mostly involving eradication of dead trees, reduced the annual loss to 500,000 m^3. Loss was kept at this level during the 1950s and 1960s but annual losses in the 1970s again exceeded 1 million m^3.

In 1979 the heaviest loss of timber, 2.4 million m^3, was recorded. The increased loss might be due to several factors. The nation's economic and social development caused drastic changes in the demand for pine timber. The price and utilization fell. Consequently, attempts to control the disease were neglected and dead trees were left in forests to become a source of new infections and increased vector production. Since 1975 the disease has spread to northern Honshu and to inland mountain-

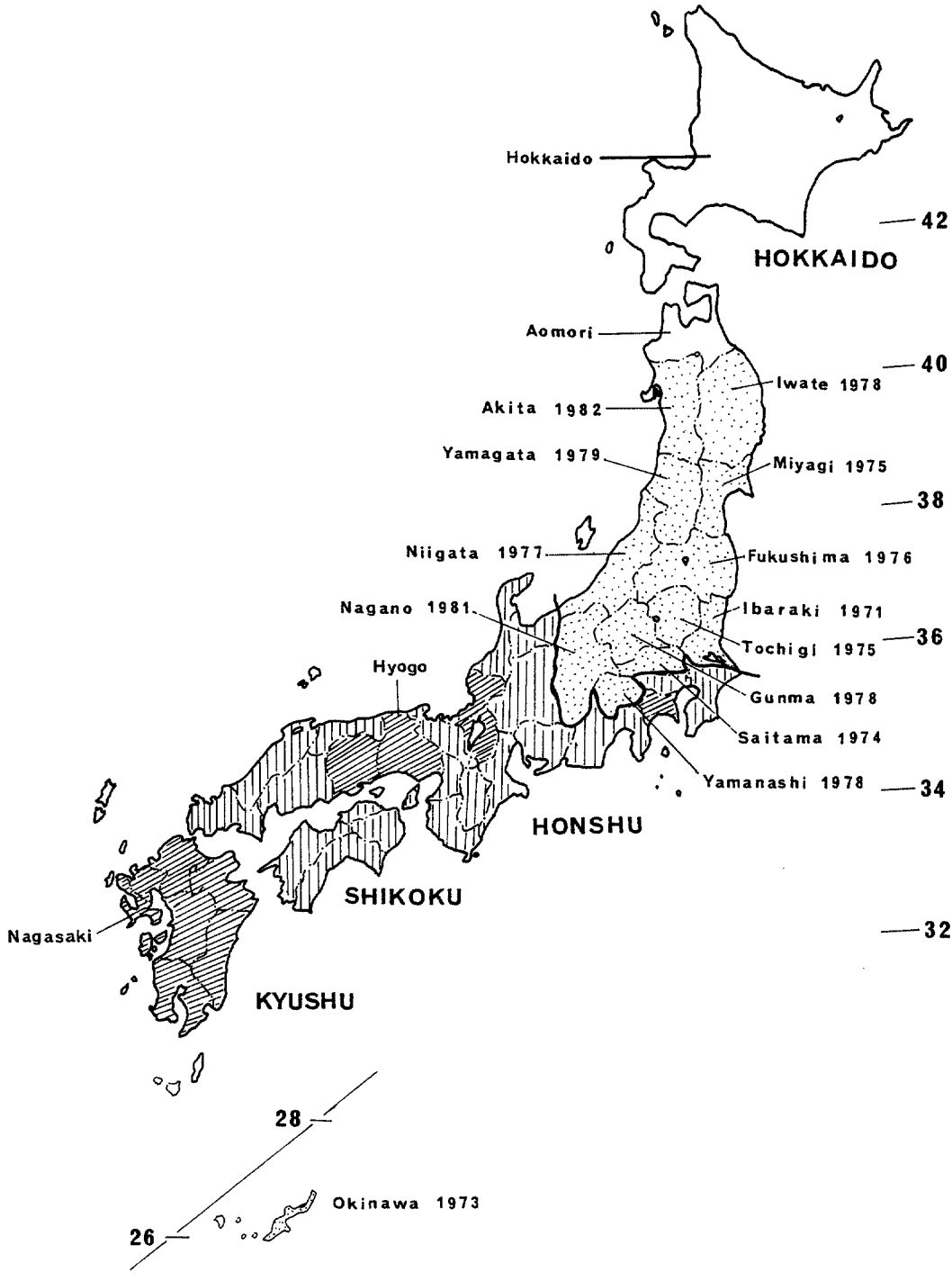

FIG. 2. The spread of pine wilt disease: ▨ during the 1930s, ▩ during the 1940–1960s, and ▩ after 1971. The year the disease first occurred is indicated for each prefecture.

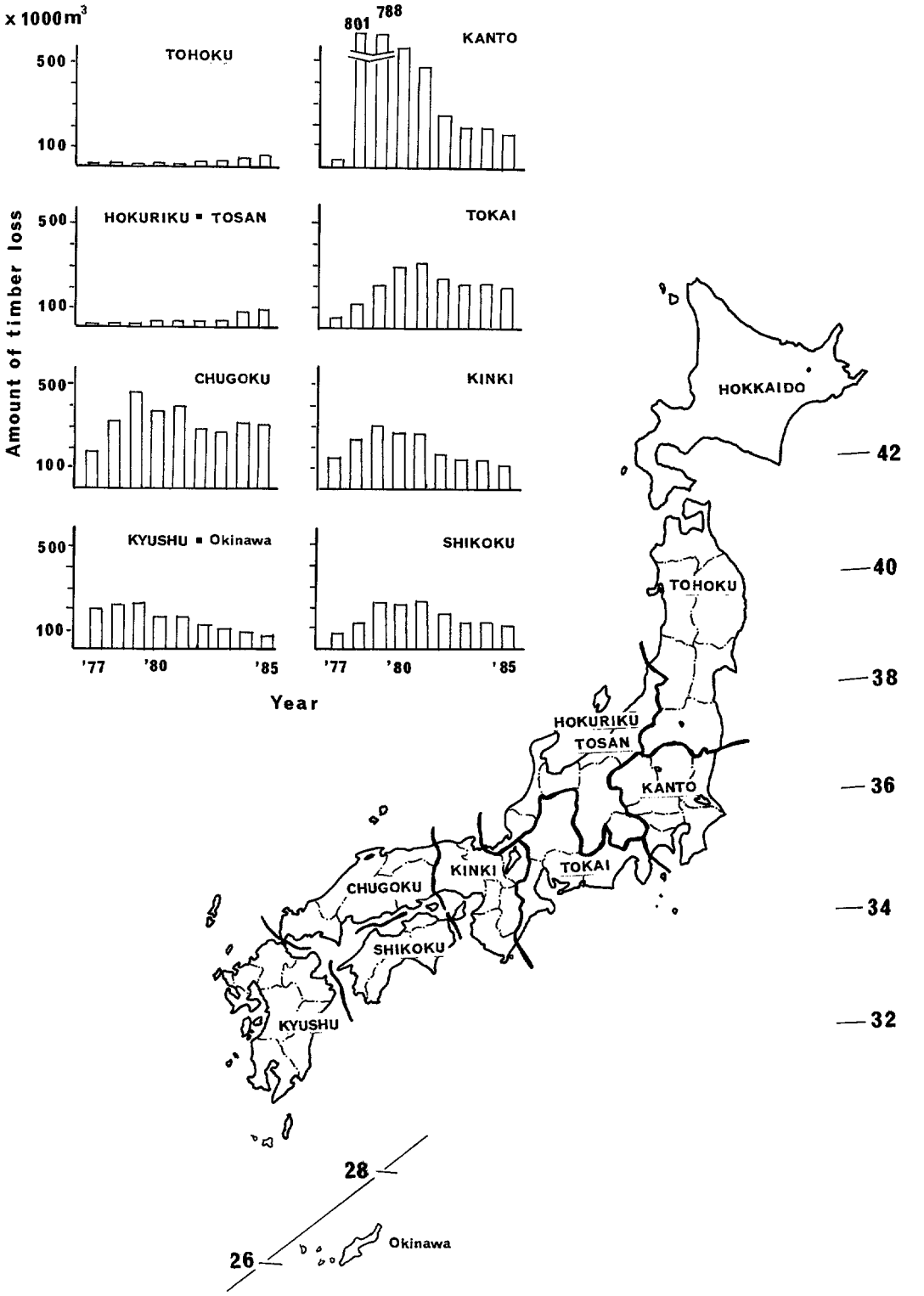

FIG. 3. Annual loss of pine trees in each district. Each district indicated in the figure is not an administrative unit but a convenient one to represent a region. (Forestry Agency, Japan.)

ous areas. This may have resulted in the recent spread of the disease from west to east and from lowlands along the seacoast to inland areas at higher elevation. Outlying infection, resulting from the introduction of nematode-infected pine logs, is a common occurrence in uninfested areas.

Since 1971 pine wilt disease has spread throughout 45 prefectures (Fig. 2), but not in Aomori and Hokkaido. An enormous increase in timber loss during this period was due mostly to the rapid increase in damage in several prefectures where the disease invaded uninfested areas. Ibaraki prefecture is a good illustration. In 1971 the disease was discovered in Mito, in the middle of the prefecture. It probably had spread from Chiba prefecture, 90 km southwest of Mito. The infested area steadily expanded until it covered almost the entire prefecture (4). In 1978 a timber loss of 742,000 m^3 in Ibaraki prefecture was almost one-third of the nation's total loss of 2.1 million m^3. Sixty-five percent of the 56,000 ha of pine forests in the prefecture were affected by the disease, and 10% of the total volume of growing stock was lost within a year. The disease progressed so rapidly that a forest without any control activities was destroyed within 4 years. Tottori prefecture had 230,000 ha of forest, including 52,000 ha of pine forest with 7,000,000 m^3 of growing stock in the late 1970s. In 1979, 130,000 m^3 of pine trees were lost, some 2% of the growing stock.

Japan has 2.6 million ha of pine forest, 10% of the nation's total forest land, with 200 million m^3 of growing stock. Annual increment in pine trees is estimated to be 5–10% of growing stock; in 1979 timber loss was 10% of the increment. In 1979, 650,000 ha, 25% of the total pine forest area, was affected by the disease. The affected area is 6.5 times that affected in 1971. The greatest timber loss each year had been in Kyushu, almost half of the total loss in Japan, but in recent years Chugoku, in the western part of Honshu, has suffered the greatest loss. Many pine forests in Kyushu have been destroyed by pine wilt disease and have been replanted with other tree species. This contributes to the decreasing annual loss in Kyushu. In Chugoku increasing loss is mostly attributed to recent disease spread in areas along the coast of the Japan Sea and in mountainous areas where many pine forests remained uninfested until the late 1970s.

Present Status

An outbreak of pine wilt disease occurred in 1975 in a pine forest on a mountain side behind a pulp factory in Ishinomaki, Miyagi prefecture. This was the first record of the disease in Tohoku district, northern Honshu. Pine logs infested with pine sawyer beetles were detected among a pile of logs at the factory yard. Since 1975 the disease has spread into scattered localities of northern Honshu. The mean annual temperature in the areas newly invaded by PWN, including inland areas located at higher elevation in central Honshu, is 10–12 C, whereas mean temperature is higher than 14 C in the areas where the disease is widespread and very damaging. The disease is becoming more widespread in cooler areas; however, the volume of timber loss is not comparable to that in warm areas (Fig. 3). Pine forests in Tohoku district are more important economically than in other areas and are generally healthy. Because pine wilt disease is not widespread in cool areas, the prevention of its invasion of these areas has priority over many problems associated with the disease in the warm region. Research efforts are concentrating upon the epidemiological aspects of the disease in northern Honshu and the central mountainous areas.

In cool areas, disease development in individual trees and the disease spread pattern, related to the vector's activities, are very different from those in heavily affected warm regions. Adult pine sawyers emerge from dead pine trees and undergo a maturation feeding on twigs of healthy pine trees during May to July. This is the common period of transmission of PWN to healthy pine trees in warm areas (7). From

mid-July to mid-August diseased trees progressively appear, and over 90% of diseased trees die by October (10,13). In cool areas, nearly half of the diseased trees do not die within the year of infection (2,4,18). These trees die in early spring to early summer the following year. According to observations by Kishi (4), most trees that died in the spring had been diagnosed as diseased late in the previous autumn. Therefore development of disease after infection occurs is delayed in cool areas. This delayed disease development is termed biennial disease development to differentiate it from that in warm areas. Biennial disease development also was observed on the trees which had not shown any symptoms the previous autumn. Inoculation experiments conducted in the northern region revealed that biennial disease development occurs in trees that are infected after August (17). Thus, under natural conditions, delayed PWN infection of trees might be responsible for this biennial type of disease development.

The effect of low temperature on disease development was demonstrated by inoculation experiments. No disease occurred on pines kept below 20 C after inoculation (5). Disease development is delayed by controlling the temperature (1): The disease can be initiated at 25–30 C and subsequently controlled by reducing the temperature to 18–20 C; disease development is reactivated and symptoms appear on nematode-inoculated trees if the temperature is increased again. These results provide evidence that delayed disease development of naturally infected pine trees in cool areas can be attributed to the effect of low temperature.

In northern regions, death of only a few branches caused by PWN is commonly observed (15). This was observed also in the United States and was called the early developmental stage of the disease, because in most cases tree death followed branch death within 2 years (8). In northern Japan, tree mortality does not necessarily follow the death of tree parts. These dead parts of trees tend to be overlooked among healthy trees and may serve as infection reservoirs because they are commonly infested with pine sawyers.

Population dynamics and distribution of *B. xylophilus* in diseased trees are different in biennial disease development and in tree death that occurs within the year of infection. In the latter case, nematode population levels increase greatly following the disease development and distribute throughout the entire tree (9). Surveys of trees dead from biennial disease development indicated that the nematode distribution was commonly limited to only a part of these trees (16). Nematodes often cannot be detected in wood collected from the basal part of such diseased trees. In addition, with delayed death syndrome trees are not infested with pine sawyer because the oviposition period of pine sawyer adults has passed when the trees become diseased. Trees affected with biennial disease development probably cannot serve as infection sources for the new season. On the other hand, pines with biennial wilt retain the ability to become infection sources for the next year. These pines remain fresh enough to provide oviposition sites for newly emerged pine sawyer adults.

The life cycle of pine sawyer in Tohoku district differs considerably from that in warm areas (7,18). Adult emergence in cool areas is more than a month behind emergence in warm areas. Adults begin to emerge the latter part of June in Tohoku district, whereas in Kyushu they start to emerge in early May. The span of emergence in northern regions is about 1 month, whereas in warm areas it is 2 months. Oviposition in Tohoku district lasts from late July to October, whereas the oviposition period in Kyushu begins early in June and lasts into September. In warm areas, early oviposition and high temperatures in summer result in larval development that brings almost all hatched larvae to the fourth instar before winter. In cool areas, late oviposition and temperatures too low for larval growth result in overwintering at relatively young stages, the second or third instar. Those larvae survive for a year in

the sapwood of dead pines and complete their cycle in 2 years.

M. alternatus usually has one generation a year, but occasionally there is a 2-year generation. The percentage of 2-year-generation adults among total numbers of emerged adults increases greatly in cool areas. It exceed 50% in Tohoku district and reaches 70–80% in the northernmost areas. A high percentage of 2-year generation times is a distinct characteristic of the pine sawyer's life cycle in cool areas and distinguishes it from the life cycle in warm areas. Pine sawyer adults take 2 years to complete a life cycle and emerge from dead pine trees holding dauer juveniles of *B. xylophilus* in their bodies. According to accumulated data, however, they carry considerably fewer dauer juveniles than do pine sawyer adults which have one generation a year. In addition, the calculated reproduction rate of pine sawyer was considerably less in cool areas than in warm areas (3). These ecological aspects of pine sawyer in cool areas are necessarily related to epidemiology of pine wilt disease. The cool summer temperature appears to be the primary factor limiting spread and development of the disease in the northern and central mountain regions. Accumulated information from studies of pine wilt disease epidemiology in cool areas allows speculation on the disease distribution and damage in the future, and this will provide the basis for establishing effective control strategy for the disease in these regions.

Perspectives of Pine Wilt Disease

In 1977 the Japanese government issued a Special Law in Force, effective for 5 years for pine wilt disease control. This special law was extended in 1982 and again in 1987. This continued the national control project for reducing pine losses and stopping disease spread, especially in newly infested areas of the northern regions. Aerial spraying of organophosphate or carbamate insecticides on a large scale was a major control method in this national project. Over a 10-year period an average of 123,000 ha of pine forests, equivalent to 20% of the total infested areas, were sprayed annually. The annual budget for the national project in 1986 was 6 billion yen, 55% of which was for aerial spraying, 8% for ground spraying, and the rest for eradicating nematode-infected dead trees by felling them followed by chemical treatment or chipping or burning the dead logs in order to eliminate the infection sources. The newly extended law puts special emphasis on pine forests closely associated with the public interest. Priority control is focused on pine forests which play a role in erosion control, water conservation, sand stabilization, wind protection, and so on. Pine forests planted on poor sites where tree species other than pine cannot be expected to grow successfully in afforestation are also the object of this special control project. Pine forests furnishing spectacular sights in recreational areas are also protected. The new law focuses on pine forests now at a primary stage of infestation in the northern regions and inland mountain areas where infection centers have just been established. Complete eradication of infection sources before the disease begins to spread is one aim. In heavily infested areas, conversion of pine forests to other tree species will be encouraged in order to keep the forest resources at a desirable level and to maintain the function of forests in land conservation.

The disease epidemiology in Japan and outside Japan suggests that *B. xylophilus* is not native to Japan. Therefore pine wilt disease caused by PWN will continue to expand into uninfested areas and loss will increase if action to control the disease is not taken. In warm areas, such as Kyushu, damage has eliminated many pine stands, and in most cases they have been replaced with natural forests of broadleaved trees. Annual afforestation with pines decreased from 41,000 ha in 1955 to 2,000 ha in 1985, whereas total annual afforestation decreased only by one-third in the same period. Pine timber production in 1985 (3.8 million m^3) was a quarter of that in 1955.

The final resolution for controlling plant disease caused by exotic pathogens should rely on either complete eradication of the pathogens or resistance breeding strategies. In addition to the national project of breeding resistant clones of native pines, which is in progress, research on resistance mechanisms involved in the relationship between the pathogen and host pines should be emphasized strongly in order to control pine wilt disease.

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