

Invasive Insect and Nematode Pests from North America

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Abstract

Of 447 alien insect, phytophagous mite, spider and nematode species in Japan, 415 are insect species. Most were introduced after the end of the Edo period (1859). Coleoptera, Hemiptera, Lepidoptera, Diptera and Hymenoptera represent the major taxonomic groups in decreasing order of number of species. They include 58 insect and nematode species from the United States. Among them, the following three have been the most devastating North American species: the pine wood nematode, *Bursaphelenchus xylophilus* (the causal agent of pine wilt diseases transmitted by the Japanese pine sawyer, *Monochamus alternatus*), which was introduced in 1905; the fall webworm, *Hyphantria cunea* (introduced in 1945); and the rice water weevil, *Lissorhoptrus oryzophilus* (1976). Their range expansions and population dynamics after their establishment in Japan have been elucidated. Explosive range expansions have always been associated with outbreaks of invasive insects. Changes in future distribution ranges under global warming are discussed. Currently those introduced species are becoming endemic as a result of various eco-physiological processes occurring after their establishment.

Key words: *Bursaphelenchus xylophilus*, exotic insects, fauna, *Hyphantria cunea*, Japan, *Lissorhoptrus oryzophilus*, *Monochamus alternatus*, range expansion, USA

1. Introduction

Exotic pests are on the increase because of growth in international air transport and tourism and increased international trade in agricultural products, and also because of growing human-dominated areas of disturbed habitat (Kiritani, 2001; Kiritani & Yamamura, 2003).

Despite the deterrent effect of plant quarantine regulations, accidentally introduced alien insect pests continue to be added to the fauna of Japan (Morimoto & Kiritani, 1995; Kiritani, 1998, 1999). Kiritani and Morimoto (1993) and Morimoto and Kiritani (1995) listed 324 species including 85 “possible” exotic species of insects in Japan. Most of the species in the latter group had been introduced to Japan before the end of the Edo period (1859) when Japan started conducting trade with Europe and the USA. Those “possible” alien species are called as “cryptogenic species” (Carlton, 1996), meaning neither native nor alien. Taking advantage of this unique political event, we define “native” by reference to a cut-off

date, i.e., 1859. Any species not already present in Japan that was introduced after that date is deemed non-native. After that time, a large number of supplies were brought into Japan from abroad, accompanied by many kinds of alien insects.

Sometimes there is insufficient information available for analysis of exotic insect species. The number of exotic species whose probable time of invasion is known is only 45% of the total and those whose country of origin is known are only 40% (Kiritani & Yamamura, 2003).

Of a total of 447 alien insect, phytophagous mite, spider and nematode species (Kiritani, 2002), no less than 58 species originated from North America. Among them, three species that have had a great impact on Japan are the pine wood nematode (*Bursaphelenchus xylophilus*: Parasitaphelenchidae, Nematoda), the fall webworm (*Hyphantria cunea* (Drury): Arctiidae, Lepidoptera), and the rice water weevil (*Lissorhoptrus oryzophilus* Kuschel: Curculionidae, Coleoptera). These three species belong to different taxonomic groups and have unique life

histories.

Each of them has inflicted devastating damage to plants that characterize typical scenery in Japan, namely, pine trees, cherry trees, and rice plants, respectively. The magnitude of the damage they have caused has been so great that it is possible to analyze and compare their biological performance with the help of information from various sources. Case histories of these three highly damaging pests may give us some ideas on vectors and pathways of invasive alien species and what happens in ecosystems newly affected by biological invasions.

2. Introduction of Alien Insects in Japan from the USA

Despite the deterrent effect of plant quarantine regulations, accidentally introduced alien insect pests continue to be added to the fauna of Japan. Kiritani (2000) published a list of 45 insect species and a nematode that have invaded Japan from the United States. Later, other species were added to the list. The cumulative number from the United States amounted to 55 species as of 2003 (Table 1). The 55 species are comprised of 21 species of each of Hemiptera and Coleoptera, 4 of Diptera, 3 of each of

Table 1 Introduced species from the United States of America excluding natural enemies introduced for biological control. Some species invaded Japan via other areas such as Pacific islands. Insects: 57spp. Nematode: 1sp.

Order	Species	Year found	Source
INSECTA			
Isoptera (3spp.)	<i>Incisitermes minor</i>	1975	Mori (1976)
	<i>Incisitermes immigrans</i>	1995	Ohmura & Tokoro (2003)
	<i>Zootermopsis nevadensis</i>	2000	Ohmura & Tokoro (2003)
Thysanoptera (2spp.)	<i>Frankliniella occidentalis</i>	1990	Kiritani (2000)
	<i>Echinothrips americanus</i>	1999	Itoh & Ohno (2003)
Hemiptera (21spp.)	<i>Antonina graminis</i>	1971	Kiritani (2000)
	<i>Aphis oenotherae</i>	1990s	Kagawa <i>et al.</i> (pers.com.)
	<i>Bemisia argentifolii</i>	1989	Kiritani (2000)
	<i>Corythucha ciliate</i>	2000	Ishikawa (pers.com.)
	<i>Eriosoma lanigerum</i>	1872	Kiritani (2000)
	<i>Genaparlatoria pseudaspidiotus</i>	?	Kiritani (2000)
	<i>Hypogeococcus spinosus</i>	1970s	Kiritani (2000)
	<i>Hysteroneura setariae</i>	1982	Sugimoro (1995)
	<i>Icerya purchasi</i>	1908	Kiritani (2000)
	<i>Illinoia liriodendri</i>	1991	Sugimoto (1999)
	<i>Kermes galliformis</i>	before 1986	Kiritani (2000)
	<i>Lepidosaphes ulmi</i>	1860s	Kiritani (2000)
	<i>Melanaspis marlatti</i>	?	Kiritani (2000)
	<i>Melanaspis obscura</i>	before 1986	Kiritani (2000)
	<i>Nearctaphis bakeri</i>	1970	(Sugimoto pers.com.)
	<i>Trialeurodes packardi</i>	1974	Kiritani (2000)
	<i>Trialeurodes vaporariorum</i>	1974	Kiritani (2000)
	<i>Uroleucon nigrotuberculatum</i>	1991	Otake (1999), Kiritani (2000)
	<i>Uroleucon erigeronensis</i>	1981	Sugimoto (pers.com.)
	<i>Viteus vitifolii</i>	1882	Kiritani (2000)
	Coleoptera (21spp.)	<i>Acanthoscelides obtectus</i>	1951
<i>Adalia bipunctata</i>		1993	Kiritani (2000)
<i>Araecerus fasciculatus</i>		1956	Kiritani (2000)
<i>Bruchus rufimanus</i>		1926	Kiritani (2000)
<i>Buprestis aurulenta</i>		1940	Kiritani (2000)
<i>Callosobruchus maculatus</i>		1950s	Kiritani (2000)
<i>Diaachus auratus</i>		1995	Kiritani (2000)
<i>Epilachna varivestis</i>		1996 (1994?)	Kiritani (2000)
<i>Euscepes postfasciatus</i>		1947	Takara (1954)
<i>Hypera postica</i>		1982	Kiritani (2000)
<i>Hypera punctata</i>		1978	Kiritani (2000)
<i>Lebia viridis</i>		1989	Kiritani (2000)
<i>Lissorhoptrus oryzophilus</i>		1976	Kiritani (2000)
<i>Listroderes costirostris</i>		1942	Kiritani (2000)
<i>Olla v-nigrum</i>		1987	Kiritani (2000)
<i>Ophraella communa</i>		1996	Kiritani (2000)
<i>Psyllobora vigintimaculata</i>		1984	Kiritani (2000)
<i>Sitona cylindricollis</i>		1961	Kiritani (2000)
<i>Sitona flavescens</i>		1986	Kiritani (2000)
<i>Sphenophorus venatus</i>		1979	Kiritani (2000)
<i>Stenopelmus rufinasus</i>		1987	Kiritani (2000)
Hymenoptera (2spp.)	<i>Sceliphron caementarium</i>	1945	Kiritani (2000)
	<i>Solenopsis geminata</i>	1967	Kiritani (2000)
Diptera (4spp.)	<i>Hermetia illucens</i>	1950	Kiritani (2000)
	<i>Liriomyza sativae</i>	1999	Kiritani (2000)
	<i>Liriomyza trifolii</i>	1990	Kiritani (2000)
Lepidoptera (2spp.)	<i>Liriomyza huidobrensis</i>	2003	
	<i>Hyphantria cunea</i>	1945	Kiritani (2000)
	<i>Parapediasia teterrella</i>	1964 & 1970	Kiritani (2000)
NEMATODA	<i>Bursaphelenchus xylophilus</i>	1905	Kiritani (2000)
Tylenchida (1sp.)			

Isoptera, and 2 of each Lepidoptera, Hymenoptera and Thysanoptera. They are arranged by their year of detection in chronological order with an interval of 10 years, except for four species whose times of introduction are not known (Table 2). The total number of species becoming established per 10 years in Japan has also increased during the past 140 years. It is possible to divide the 140 years into the following three phases in terms of the frequency of invasions, 1860–1939, 1940–1969 and 1970–1999. The frequency of invasion during 1970–1999 was as high as 10 times that in 1860–1939, and it is expected that one new species will become established in Japan every year.

In the following accounts, we elucidate the invasive histories of three exotic species originating from the USA. Each of them demonstrates unique characteristics in terms of range expansion, population dynamics, and evolutionary perspective. They also represent pests of forests, urban areas, and agricultural crops, and invaded Japan in 1907, 1945 and 1976, each representing three different phases of invasions in Table 2.

3. Pine Wilt Disease

Pine forests in Japan occupy about 2.5 million ha, accounting for about 10% of forested land. Pine trees have been economically important from ancient times, mainly as fuel for domestic and industrial uses and as lumber for building. The decline of pine forests in Japan has seriously affected soil and water conservation and, consequently, agriculture and aquaculture. Loss of ornamental pines to pine wilt disease has had an impact on Japanese culture as well (Kobayashi *et al.*, 1984; Kobayashi, 1988).

Epidemics of pine wilt disease caused by the pine wood nematode (PWN), *Bursaphelenchus xylophilus*, whose vector is the Japanese pine sawyer (JPS), *Monochamus alternatus*, are killing pine forests throughout Japan. The major pine species, Japanese red pine (*Pinus densiflora*) and Japanese black pine (*P. thunbergii*) have suffered heavy mortality for several decades. The foliage of infected trees quickly fades to a reddish-brown. Most trees naturally infected with nematodes die within a year of infection, usually by late autumn, in warm temperate climatic zones (Fig. 1).

Ecological and biological characteristics of the two

Table 2 The number of species which invaded Japan from the US.

Period	No. species	No. species/year
1859–1939	6*	0.1
1940–1969	11	0.4
1970–1999	33**	1.1

*: including the pine wood nematode.

** : three species invaded after 2000.

key species are as described below.

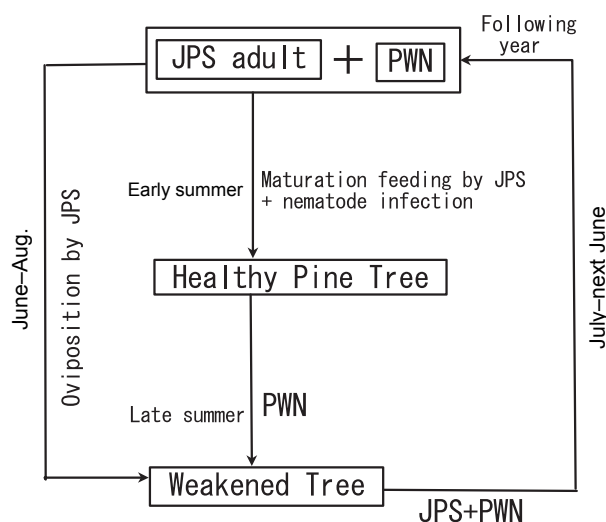
PWN (*Bursaphelenchus xylophilus*): Widespread distribution of this nematode was reported in the United States (Wingfield *et al.*, 1982), where only exotic pine plantings are severely damaged, suggesting that the nematode could have been accidentally introduced into Japan from the United States. This view has been supported by DNA sequence comparison between isolates of *B. xylophilus* from both countries (Harmey & Harmey, 1993; Tarès *et al.*, 1993). Nagasaki, where the first pine wilt disease outbreak was recognized in 1905, was the most prosperous international trading port at that time.

JPS (*Monochamus alternatus*): The JPS has been recorded in mainland China, Taiwan, Laos, Korea (Cheju Is.), and Japan (Table 6). It normally produces one generation a year and is widely distributed in Japan, except for Hokkaido and northern Honshu. Its distribution in both Okinawa Prefecture and the Ogasawara Islands is considered to be due to recent introductions of infested pine logs. The factor limiting its distribution in northern Honshu is the lack of sufficiently high temperatures in summer, not the low temperatures in winter (Makihara, 1997).

3.1 Epidemics of pine wilt disease

The decisive factor in developing epidemic infestation in Japan was the contact between sawyers and nematodes. The JPS is native to Japan but was a rather scarce insect until it came into contact with the PWN. The spread of disease is facilitated by an obligatory mutualism between PWN and JPS: the JPS helps the PWN be transmitted to a new host tree, while the PWN supplies the JPS with newly killed trees on which to lay eggs (Fig. 1).

The JPS adults emerge in early summer and feed on young twigs for maturation, meanwhile PWN dauerlarvae invade healthy pine trees. Once within



JPS : Japanese pine sawyer *Monochamus alternatus*
 PWN : Pine wood nematode *Bursaphelenchus xylophilus*

Fig. 1 Epidemic cycle of JPS-PWN-Pine tree.

the plant, the nematodes reproduce rapidly and the infected tree shows symptoms of decline about three weeks later (Kobayashi *et al.*, 1984). The weakened pine trees provide JPS females with oviposition sites. Dead trees are not available for oviposition and will never serve as infection sources again. Once the nematode is introduced into the sawyer – pine tree system, the beetle increases its own food supply by transmitting nematode during maturation feeding, resulting in an unstable interaction system (Fig. 1). Consequently during a four-year study the net reproduction rate (R_0) of the JPS varied greatly from 5- to 11-fold (Togashi, 1989). A 10-year-old plantation of *Pinus thunbergii* located in central Honshu exemplifies the epidemic (Table 3) (Kobayashi, 1978). The annual mortality of pine trees was about 5% in a stand free from the PWN, while stands infected by the PWN resulted in mortalities of 25% in Hiroshima, and 17%, 37% and 44% in Ibaraki, giving 30% as a mean mortality (Togashi, 2002).

3.2 Range expansion

After a latent period of two decades, the infestation spread rapidly through Kyushu into western Honshu. During the war, annual tree losses increased, reaching 1.3 million m^3 in 1948. Outbreaks were encouraged by the collection of turpentine oil from pine trees which provided weakened trees for oviposition. Control operations helped by the utilization of killed trees as fuel resulted in decreased infestation in the 1950s. At the beginning of the 1970s, however, the rate of infestation started to rise again because of the change to petroleum as Japan's major energy source and a lack of labor for control operations. In 1978 and 1979, largely because of hot, dry summers that encouraged epidemics, annual tree losses amounted to 2 million m^3 /year (Fig. 2). In 1979, 650,000 ha, 25% of the total pine forest area, was affected by the disease, and the annual loss of timber reached a record-breaking 2.4 million m^3 . A nationwide control project was started in 1977 and about \$30 million is now spent annually on spraying and treating infested logs. Annual tree losses have gradually decreased, but infestations have spread into northern Honshu and into forests at higher elevations (Fig. 2 & Fig. 9, left).

In general, both temperature and precipitation are important factors that affect the severity of damage by

PWN. High temperature and low precipitation in summer cause accelerated damage. Because of their effects on feeding by JPS adults, the propagation of PWN and water stress on trees. Pine trees infected with PWN show cessation of oleoresin exudation, a symptom of disease, over the period from June to October (Mamiya, 1983). Females that emerge from dead trees in June and July lay eggs on weakened trees until September. Therefore, the extent to which their oviposition and the appearance of weakened trees overlap is decisive in determining the severity of the epidemics. Delayed appearance of weakened trees in a cool and rainy summer climate, therefore, results in a less intense epidemic (Togashi, 1989).

An MB index that combines temperature conducive to JPS development, PWN infection and tree weakening has been proposed as a measure of infestation potential (Taketani *et al.*, 1975). This is the annual summation of residues of mean monthly temperature exceeding 15°C. Epidemic pine infestations nearly always correspond to areas with an MB index exceeding 40. Such areas are located mainly along the coast and inland along river valleys up to about 200 m above sea level. In general, damage due to the PWN hardly ever occurs in areas where the monthly mean temperature from June to August is below 20°C.

3.3 Pathogenic variability

When tested on 4-year-old Japanese black pines in Japan, the virulence of 37 populations of PWN varied from 0 to 100% in terms of pine tree mortality. Four of the most virulent populations were recovered from northern Japan where establishment was relatively recent (Kiyohara & Bolla, 1990). In the USA where the PWN is native and widely distributed, the occurrence of pine wilt disease is rarely observed, except in the case of some exotic pine plantings. It is known that *Pinus strobus* and *P. taeda* are resistant to the PWN infection (Kiyohara, 1997).

The myxoma virus, introduced into Australia to control rabbits, underwent a rapid attenuation of virulence, measured in terms of lethality to a standard susceptible population (Fenner & Ratcliffe, 1965). It is our concern whether and when the current unstable system of pine wilt disease will become stabilized. That less virulent races have been found more

Table 3 Annual change of pine tree mortality in a severely infested forest located at Hikigawa, Wakayama (Kobayashi, 1978).

	1967	1968	1969	1970	1971	1972	1973	1974
No. of trees living at the beginning of the year	455	435	379*	237*	52*	23*	4	0
No. of trees killed	20	54	141	179	15	19	4	
% trees killed	4	12	37	73	29	83	100	

* No. of trees is not equivalent to the remainder subtracted from the number in the previous year because of felling of living trees alive.

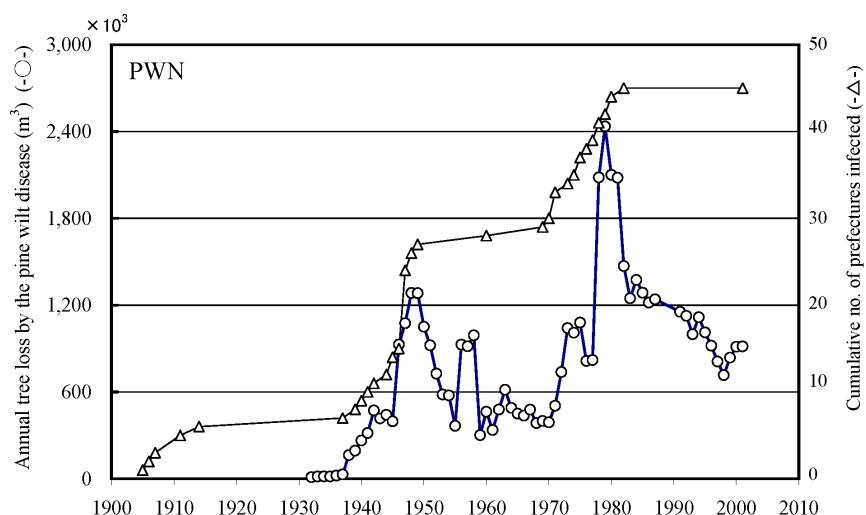


Fig. 2 Annual changes in pine tree loss due to pine wilt disease (-○-) and in the cumulative number of prefectures infected by the PWN (-△-) (revised by Kishi, 1988).

frequently in southwestern Japan where epidemics occurred earlier, and that pine trees which survive an epidemic are more resistant to the disease (Toda, 1997) suggest the possible existence of moderate virulence once the feedback between ecological and evolutionary processes is incorporated into the system (Lenski & May, 1994; Togashi, personal communication). It is still too early to predict when the current epidemics will shift to an endemic state, because only 100 years (a few generations of pine stands) have passed since the PWN invaded Japan.

4. The Fall Webworm (FWW), *Hyphantria cunea*

4.1 Invasion and range expansion

In North America, the fall webworm (FWW), *Hyphantria cunea*, is found over a wide area extending from Canada to Louisiana. The FWW occurred only in North America before 1940, but was subsequently introduced to central Europe and eastern Asia during the 1940s by human activities (Warren & Tadic, 1970). Two color forms of the FWW are known in North America. The type introduced into Japan, as well as into Korea and Europe, belongs to the black-headed form and is quite distinct from the red-headed form reported from Louisiana (Oliver, 1964; Itô & Hattori, 1973).

The FWW was first found in Tokyo (35.7°N) in 1945, two months after the end of World War II (Table 6), and since then has caused great damage to garden and roadside trees. It has spread along highways and railways in association with its outbreaks (Masaki, 1975). The first outbreak lasted from 1945 to 1957, and the second, from 1964 to 1968 after an endemic stage from 1958 to 1964 (Itô & Miyashita, 1968) (Fig. 3). The number of prefectures infested by the FWW in the second outbreak reached 21 (Fig. 3). Thereafter, the rate of expansion decreased, with sporadic

occurrences in neighboring prefectures. The present distribution ranges from 32°N to 41°N, covering at least 35 of the 47 prefectures in Japan (Gomi, 1999) (Fig. 9, middle).

4.2 Population dynamics and natural enemies

An outstanding feature of FWW infestations is that the occurrence of FWW is rarely observed in forests, but is confined to trees along roadsides and in residential areas. The failure of FWW to invade forests is due to predation pressure by birds and other polyphagous predators. The factor responsible for keeping the population density low during 1958–1964 was those natural enemies of FWW (Itô & Miyashita, 1968). Life table studies conducted by Itô and Miyashita (1968) showed that mortality from egg to the 4th instar was 20% to 70%, while that from the 5th instar to pupa was over 96% during 1966–1969 at two experimental stations (Table 4). The low mortality rate in early stages is considered due to the protective role of the nest-web and being free from egg and larval parasitoids. Watanabe (personal communication), who conducted an intensive survey on the parasitic fauna of FWW larvae during 1995–1997 in Tsukuba, found no hymenopterous parasitoids but 6 species of tachinids that are generalists in host preference. The highest rate of parasitism due to the tachinid complex was 70%–80% in 3rd-generation larvae in the wandering stage.

Mortality during later stages is mainly due to predation by birds in the first generation and *Polistes* wasps in the second generation (Itô & Miyashita, 1968). It is interesting to compare the number of spiders inhabiting FWW webs between Japan and North America (Table 5). Two hundred fifty-five spiders, representing 34 species and 10 families, were recorded from 248 FWW webs in Tokyo (Kunimi, 1983). The mean number of spiders per web was as small as 0.37, compared to 1.26 in Arkansas (Warren *et al.*, 1967), 2.28 in New Brunswick, and 3.01 on the

coast of Nova Scotia in Canada (Morris, 1972) in the countries of origin of FWW.

The extent at which *Liquidambar styraciflua* L. trees along the roadside in Tsukuba were defoliated by the FWW correlated positively with the index of urbanization, which is expressed in terms of the proportion of plant ground cover (Fukuyama, 1996). Fukuyama (1996) considered the paucity of polyphagous natural enemies caused by urbanization as a factor in severe defoliation by the FWW.

4.3 Development of a trivoltine race

The bivoltine life cycle of the FWW in Tokyo is clearly explained by the photo-thermal reaction. In

the larval stage of the summer generation, the day length exceeds the critical level (14 hr. 35 min. at 17–27°C) and diapause is averted. It becomes shorter than the critical level for the next brood, and the pupae enter diapause and hibernate (Masaki, 1975). It is predicted that the FWW will be unable to invade Hokkaido where the available heat units could permit only one generation a year. The long days in summer, however, would prevent diapause. In the southern part of Kyushu and Okinawa, the warm climate would allow at least three or four broods a year, but the day length becomes shorter than the critical level long before winter. This would make it difficult for the

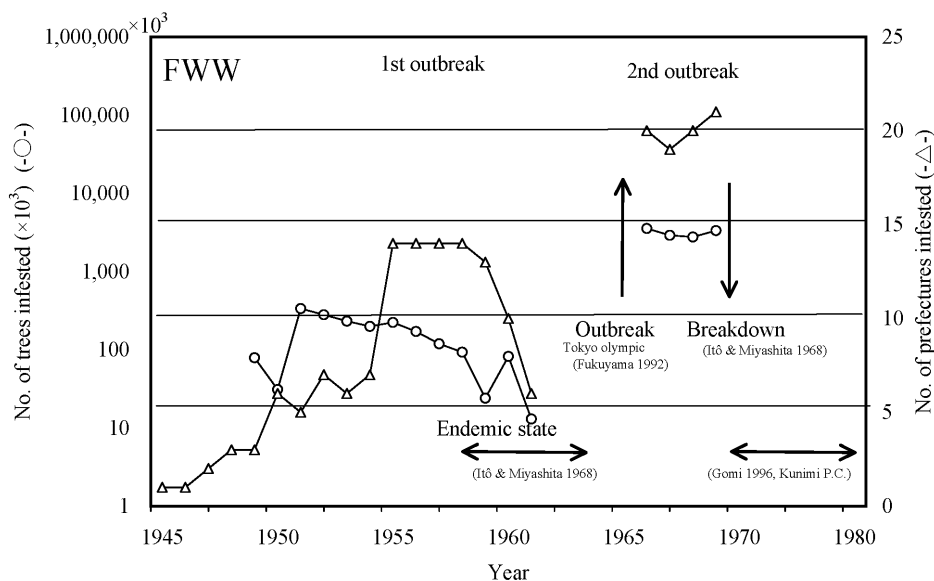


Fig. 3 Annual changes in number of trees infested by FWW (○-) and infested prefectures (-△-) in Japan.

Table 4 Mortality rates of the fall webworm in the periods from egg to 4th instar and from 5th instar to pupa observed at two experimental sites in Tokyo during 1966 – 1969. (Itô & Kiritani, 1971)

Year	Generation	Nishigahara, Tokyo		Futuyu City, Tokyo	
		Egg-L4	L5-Pupa	Egg-L4	L5-Pupa
1966	1st generation	60%	98.4%	65%	99.1%
	2nd generation	69	98.8	71	99.9
1967	1st generation	67	99.2	36	99.8
	2nd generation	61	99.6	50	99.0
1968	1st generation	61	96.4	29	97.8
	2nd generation	51	99.5	38	98.2
1969	1st generation	52	99.3	69	95.5
	2nd generation	20	99.6	58	97.7
Mean	1st generation	60	98.3	53	98.1
	2nd generation	50	99.4	54	98.7

Table 5 Mean numbers of spiders collected from nests of the FWW in different countries.

Country		No. spiders / nest	Authors
USA	Arkansas	1.26	Warren <i>et al.</i> , 1967
Canada	New Brunswick	2.28	Morris, 1972
Canada	Nova Scotia	3.01	Morris, 1972
Japan	Futuyu City, Tokyo	0.37	Kunimi, 1983

FWW to become established in Okinawa (Masaki, 1975). Masaki (1975) suggested that the seasonal life cycle may change in the future through natural selection.

Among insects inhabiting temperate areas, there is a general tendency for northern populations to enter diapause earlier in the year under longer day lengths than the southern ones (Masaki, 1975). In the mid-1970s, three decades after the introduction of the FWW to Tokyo, a partially trivoltine life cycle was reported in the southwestern part of Japan (Uezumi, 1976). Recently, trivoltine populations have prevailed in the southwestern areas and bivoltine ones in the northern areas (Gomi, 1999; Gomi & Takeda, 1996).

The critical photoperiod was longer in bivoltine populations north of 36°N than in trivoltine populations south of 36°N. The durations of the larval and pupal stages were shorter in the southern populations than in the northern ones. Thus, both the critical photoperiod and developmental rate changed when the shift in voltinism from bivoltine to trivoltine occurred as this insect expanded its range (Gomi, 1999). It has been confirmed by the DNA sequence of the cytochrome c oxidase subunit I gene that, in spite of the divergent life cycles of FWW in Japan, the variation in voltinism has been established by natural selection after introduction and is not due to multiple introductions from different parts of the USA (Ozaki & Ohbayashi, 2001). Masaki (1977) predicted that the FWW would establish a clear geographic cline in the critical photoperiod in the future. It would be interesting to find out how long it will take the FWW to form such a cline in Japan.

5. The Rice Water Weevil (RWW), *Lissorhoptrus oryzophilus* Kuschel

5.1 Invasion and range expansion

The RWW is the most common and probably the most destructive insect pest of rice in the United States. The insect in the southeastern part of the USA reproduces bisexually. The presence of RWW in the rice-growing area of California, where it reproduces parthenogenetically, was first reported by Lange

in 1959 (Bowling, 1967).

The RWW, which is likely to have invaded Japan from California, was first found on the Chita peninsula, Aichi Prefecture, in 1976 (Table 6). At that time, stock farmers on the Chita peninsula imported hay from California. The Japanese RWW reproduced parthenogenetically as in California (Tsuzuki *et al.*, 1984). It had become distributed throughout Japan by 1986. Subsequently, the RWW invaded Korea in 1988 (Lee & Chang, 1989), mainland China in 1988 (Hirai, 1996), and Taiwan in 1990 (Shih, 1991). The maximum area of rice fields infested by the RWW in Japan was observed around 1990 and amounted to 1,440,000 ha (Fig. 4).

The RWW overwinters in adult diapause which terminates by December (Morimoto, unpublished data). The overwintered adults develop flight muscles by feeding on the leaves of Gramineae and Cyperraceae plants (Okada, 1980). They invade paddy fields by crawling or flying when rice plants are transplanted. Ovarian development takes place as a result of feeding on rice plants. The larvae feed on the roots of rice plants and pupate there. Newly emerged adults disperse to overwintering sites (Asayama *et al.*, 1984).

The range expansion of the RWW in each prefecture of Japan has been described in detail (Azuma *et al.*, 1991). The spatial expansion rate of the RWW within a prefecture was calculated using a logistic equation;

$$Y = m_1 / \{1 + \exp[-m_2 \times (T - m_3)]\}$$

where Y is the area of rice fields (ha) infested by the RWW, T is the year, and m_1 , m_2 and m_3 are constants. The three parameters (m_1 , m_2 and m_3) were estimated using the least-square method. The tangent line at the point of inflection of each curve was computed as

$$R = m_1 \times m_2 / 4$$

where R is the slope of the line. The slope is defined as the expansion rate of the RWW in each prefecture. The expansion rate was significantly negatively correlated with latitude ($R = 0.76$) among the prefectures located between 30°N and 40°N (Fig. 5).

Andow *et al.* (1993) reported that the distribution boundary line varied with time and was dependent on direction. The progression rate of the boundary line

Table 6 Range expansions of the pine wood nematode (PWN), fall webworm (FWW) and rice water weevil (RWW), in Japan and to neighboring countries.

	PWN	FWW	RWW
Mainland	1905 (Nagasaki), absent from Hokkaido	1945 (Tokyo), and in 2000 in Hokkaido ¹⁰⁾	1976 (Aichi) and in 1986 in Hokkaido
Okinawa	1973 ¹⁾	absent	1985 ²⁾
Ogasawara	1974 ³⁾	1994 (trivoltine type) ⁴⁾	----
Korea	1988 (symptoms observed since 1983) ^{5) 3)}	1958 in Soul ⁶⁾	1988 ⁷⁾
Taiwan	1985 ⁵⁾	absent	1990 ⁸⁾
China	1982 ^{5) 9)}	occurs commonly ⁶⁾	1988 ²⁾

1) Kishi (1988) 2) Hirai (1996) 3) Makihara (1997) 4) Ohobayashi (2002) 5) Kiyohara (1997)
6) Gomi(1996) 7) Lee and Chang (1989) 8) Shih (1991) 9) Sun (1982) 10) Tate (2001)

was initially between 28 km/year northeastwardly and 47 km/year southwestwardly; it increased to about 274 km/year and 113 km/year, respectively, 7 years after the initial invasion.

The most important factors in the range expansion of invasive organisms are reproduction rate and dispersal ability (Hengeveld, 1989; Andow *et al.*, 1993; Williamson, 1996; Shigesada, 1992). The active adult dispersal of the RWW between hibernacula and paddy fields can be observed only in spring and late summer, because the degeneration of the flight muscle prevents RWW adults from dispersal by wing at other times (Matsui, 1985). It has been pointed out that wind plays an important role in the long-distance dispersal of the RWW (Kishimoto, 1980; Muramatsu & Tao, 1981; Tsuzuki *et al.*, 1984). In general, low-pressure air masses, typhoons, and prevailing westerlies move from west to east over the Japanese Islands. Accordingly, the founding RWW population established in central Japan may disperse eastwards with the movement of these air masses (Kobayashi & Suzuki, 1983; Kaneko *et al.*, 1984). Because it takes some time for any newly invading population to reach a detectable level of density, it is difficult to identify a causal relationship between a particular weather condition and the range expansion of the RWW.

There is a great difference in the intensity of RWW occurrence between north and south. The percentages of paddy fields infested by the RWW were 57% and 27% in Tohoku (north) and Kyushu (south), respectively, in 1995 (MAFF, 1996). Transplanting of rice occurs earlier in areas further north (Fig. 6). The RWW density is higher in localities where rice is transplanted early than elsewhere (Izawa *et al.*, 1984; Naba *et al.*, 1989; Kobayashi *et al.*, 1997). In southern Japan, invasions of the RWW used to be detected first in each prefecture in the localities where rice was transplanted earliest (Higo *et al.*, 1986; Nagai

& Teramoto, 1985; Ogawa *et al.*, 1989; Yamanaka *et al.*, 1985). These findings strongly suggest that the population dynamics of the RWW are closely related to the time of transplanting of rice.

Adults that have overwintered in northern areas can access rice plants much earlier than those in southern areas, and it is highly probable that they can realize their potential fecundity as well as enjoy a high survival rate (Figs. 7A & 7B). The flight muscles of the RWW are not fully developed by the time of transplanting of rice in northern areas, and most of the adults immigrate into the rice fields by walking (Figs. 7A, 7B & 7C). By contrast, overwintered adults are able to access to rice plants by flight in southern Japan (Figs. 7C, 7D), but their fecundity is greatly diminished due to the low survival rate and aging during the long waiting period for transplanted rice (Figs. 7D & 7E). As this process is repeated year after year, the RWW population density in northern areas becomes larger and eventually the rate of spread accelerates.

5.2 Population dynamics

Over the last decade, the RWW's rate of spread has decline and it now occurs in half of the total area of rice fields of Japan (Fig. 4). Changes in the mean total number of larvae and cocoons found per hill are shown in Fig. 4 in non-treated plots of experimental rice fields located in 11 prefectures in the Kanto and Tokai areas. The density was initially around 20 individuals per hill, and it increased up to 30 in 1985 when the RWW had spread throughout Japan (except for Hokkaido) (Figs. 4 & 9). Thereafter, it declined in a saw-tooth pattern to less than 10 in 1995 (Hirai, 2000). Recently it has again shown an increasing trend in density, but the reason remains to be known (Fig. 4). Almost the same results were obtained in Nagano prefecture in terms of the population density of overwintered adults from 1985 to 1994 (Kobayashi *et al.*, 1997).

The population density seemed to stabilize 4–5

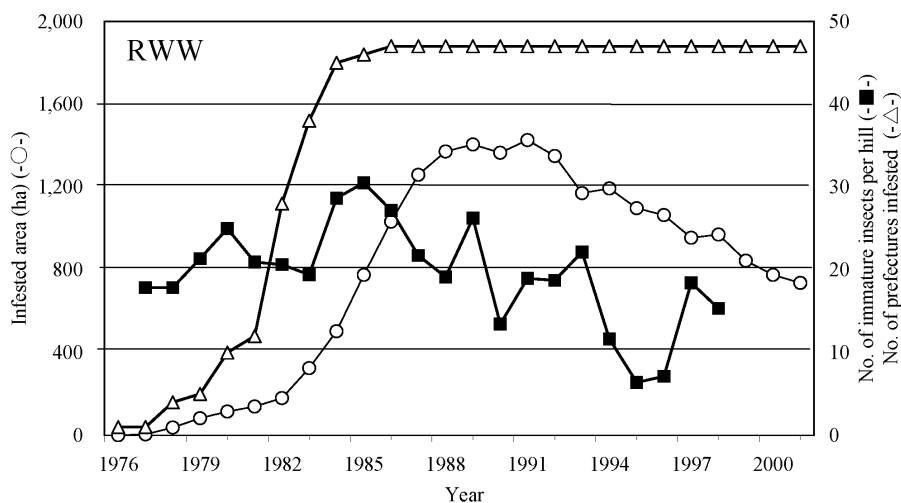


Fig. 4 Annual changes in area infested by RWW(-○-), number of prefectures infested (-△-), and the density of immature RWW per hill (-■-).

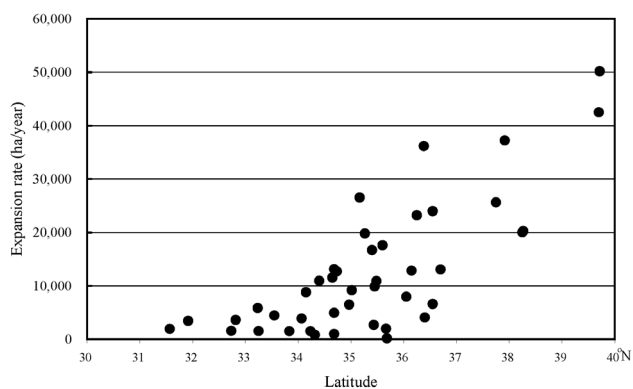


Fig. 5 Expansion rates of RWW in 44 prefectures in relation to their latitudes. The southernmost (Okinawa) and northernmost (Hokkaido and Aomori) prefectures were excluded. Each circle represents an individual prefecture.

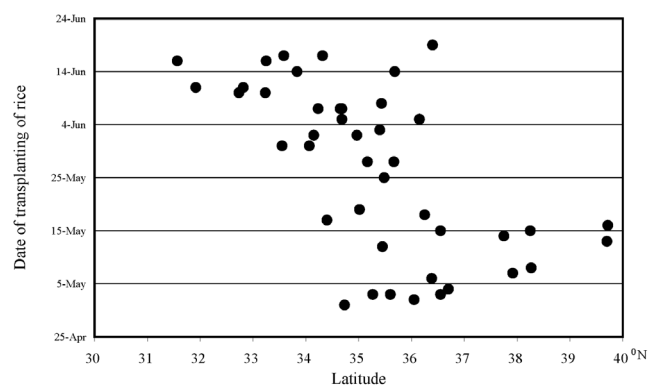


Fig. 6 Date of transplanting of rice in the 44 prefectures in relation to their latitudes.

years (generations) after invasion. The RWW population density appeared to be regulated mainly by density-dependent processes that operated between oviposition and the emergence of young larvae. Fecundity decreased with increasing density of over two adults per hill. Population density was dependent on the mortality rate from egg to young larva, and this was the key factor determining the generation mortality from egg to the emergence of the adult (Kayumi *et al.*, 1984).

The pattern of population growth can be simulated by a logistic equation:

$$(N_{t+1} + N_t) / N_t = R (1 + N_t / K)$$

where N_t and N_{t+1} are the numbers of overwintered adults per hill in years t and $t+1$, R is the rate of annual increase, and K is equilibrium density. K seems to be determined by the availability of overwintering sites and the date of transplanting or availability of rice plants for overwintered adults. K was estimated at 0.38, 1.78, and 2.44 adults/hill for coastal areas, inland hilly areas, and mountainous areas, respectively (Fig. 8) (Kayumi *et al.*, 1984).

So far, no evidence has been obtained concerning the effect of natural enemies of the RWW. This is partly due to the submerged life cycle of the RWW, which prevents us from making direct observations of

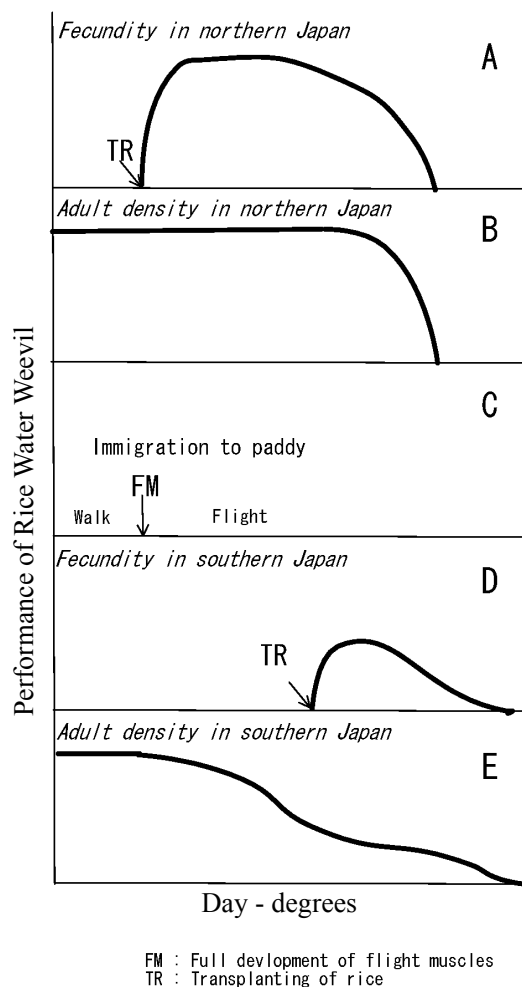


Fig. 7 Difference between southern and northern Japan in the extent to which the potential fecundity of the RWW is realized. Egg maturation occurs after feeding on rice plants.

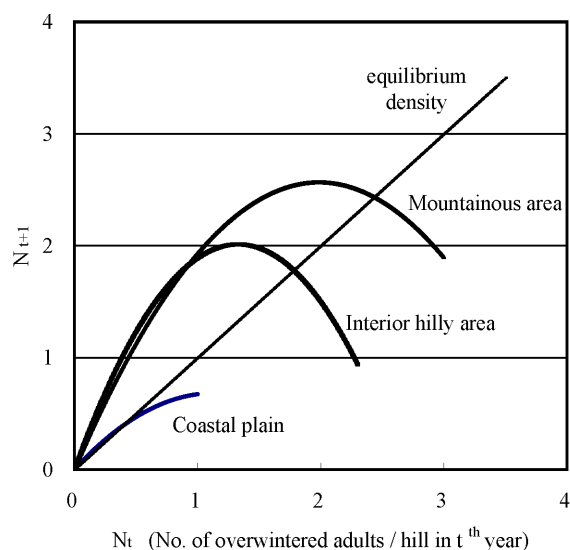


Fig. 8 Reproduction curves and equilibrium densities in the areas with different topography. (after Kayumi *et al.*, 1984).

the activities of predators. The recent reduction in the RWW population density and the size of areas infested may be largely attributable to the widespread application of pesticides to the nursery trays before the rice is transplanted.

6. Discussion

The biological process of colonization by alien organisms can be categorized in the following four steps: introduction, establishment, spread, and naturalization (Kiritani, 1998). Several attempts have been made to characterize successful and unsuccessful invaders (Kiritani, 1983; Ehrlich, 1988; van Lenteren, 1995; etc.). Characteristics of successful invaders such as polyphagy, multivoltinism, parthenogenesis, anthropogenic inhabitant, and good dispersal capability are generally accepted by most ecologists. However, there are so many exceptions that it is not justifiable to use these characteristics as reliable indicators of a species' potential to invade (Ehrlich, 1988; van Lenteren, 1995). Indeed, the RWW, a typical example of an invasive pest of agricultural crops, is univoltine and monophagous.

The range expansions of the PWN, FWW, and RWW in Japan and their hypothetical reproduction curves are summarized in Fig. 9. The FWW spread from Tokyo to other parts of Japan assisted by transportation systems or by hitchhiking. Its range expansion was limited by its genetic variability in terms of thermo-photoperiodism, which determines its life cycle in a newly invaded area.

The RWW showed a continuous diffusion with the spread rate accelerating with time. The speeds at which the RWW spread its range were 28 km/year to

the north and 47 km/year to the south in the early phase of range expansion (Andow *et al.*, 1993). The range of the RWW depends on the availability of rice plants. Therefore, it is distributed throughout Japan, including the Nansei islands (Okinawa).

The pattern of range extension of the PWN/JPS is a mixture of hitchhiking and continuous diffusion types. Hengeveld (1989) called this type of range expansion stratified diffusion, as it involves not only short-distance dispersal, but also long-distance dispersal. Takasu *et al.*, (2000) estimated the speed of range expansion as 4.2 km/year for short-distance dispersal. The PWN/JPS was prevented from spreading further by the cool, wet summers prevailing in the invaded area.

The patterns of population dynamics of the above three species were also species specific. The FWW suffered mortality due to generalist natural enemies. It showed gradation-type outbreaks when it escaped from the control exerted by natural enemies. On the other hand, there were no observations of arthropod natural enemies of the RWW. Density-dependent processes involving changes in fecundity and survival rate in earlier developmental stages were suggested as regulatory factors. The density tended to stabilize after 4–5 years of invasion, fluctuating around an equilibrium density specific to each locality.

The PWN/JPS system is unique. The JPS is attacked by microbes, nematodes, arthropod predators, and parasitoids. It is regulated by density-dependent mortality in the early larval stages (Kobayashi, 1988; Kobayashi *et al.*, 1984). When the JPS comes into contact with introduced PWN, pine wilt disease epidemics become destructive and continue until entire pine stands are destroyed.

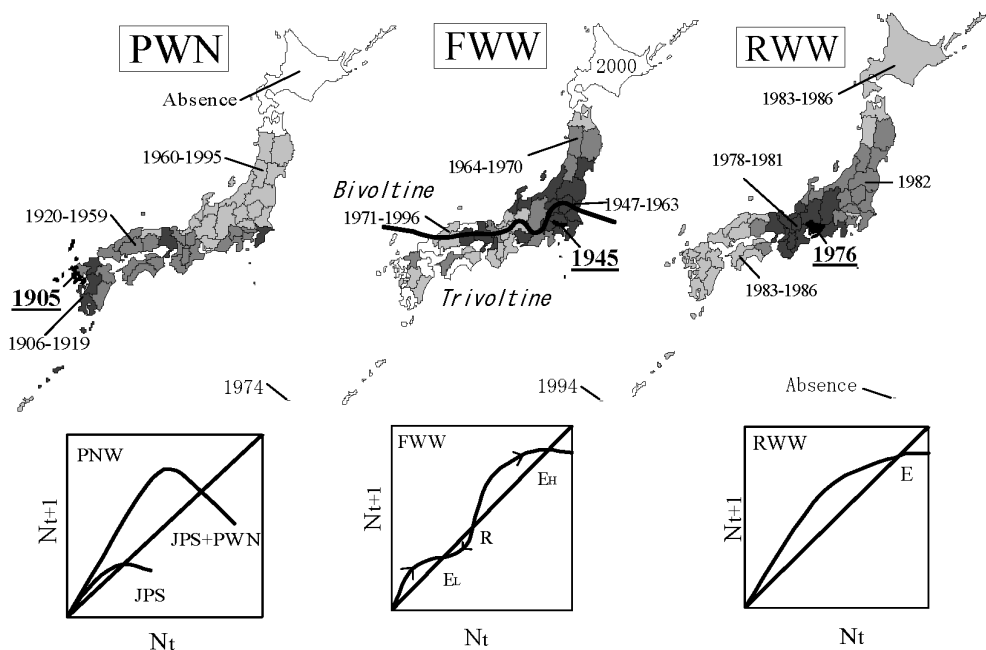


Fig. 9 Range expansions and reproductive curves of the pine wood nematode (PWN), the fall webworm (FWW), and the rice water weevil (RWW) in Japan. For range expansions, see also Table 6.

Our analyses demonstrated that ecological and physical conditions in the invaded areas were of paramount importance in determining the status of colonizers after establishment. In particular, climatic conditions, natural enemies, distribution patterns of host plants, genetic variability, and synchronization of life cycles of insects and their hosts were the factors that determined population density and the expansion rate of colonizers. Concerning the long-distance expansion of successful invaders, it should be emphasized that explosive range expansions involving neighboring countries, i.e., Taiwan, Korea, and mainland China, were always associated with outbreaks of the invasive insects in Japan.

The Intergovernmental Panel on Climate Change (IPCC) (2001) has predicted that the global-mean surface temperature will increase 1.4–5.8°C by the year 2100 as compared to 1990. Such an increase in temperature may result in an increase in number of generations per year and in a shift of the distribution range of most insects (Morimoto *et al.*, 1998; Yamamura & Kiritani, 1998). The reproductive performance of the RWW depends greatly on temperature, and the RWW lays the highest number of eggs with the shortest preoviposition period at 32°C within a temperature range of 15–32°C (Morimoto, unpublished data). In order to fully realize RWW fecundity, the existence of rice plants is essential. If the time of rice transplanting should advance accordingly, the overall population density of the RWW would be expected to increase under global warming. As the current distribution of pine wilt disease is limited by low temperatures in summer, not only would pine wilt disease extend its distribution to Hokkaido, but also the intensity of epidemics would increase in the northern part of Japan (Table 6). In the case of the FWW, the trivoltine race would become predominant even north of 36°N. Range expansion further north or south beyond the current distribution would depend on whether the FWW could adjust its temperature as well as photoperiod responses to new environmental conditions in the foreseeable future.

Current control measures

The distribution ranges of the PWN, FWW and RWW cover almost all of Japan. Because it is impossible to eradicate them, we must adopt an IPM strategy to control them. In this section, current control measures were reviewed.

PWN: The JPS which serves as the vector for the PWN has been controlled with insecticides. Aerial spraying of insecticides by helicopter was commonly practiced in some parts of Japan. This widespread chemical control may seriously affect the biodiversity of pine forests. Trunk injection of nematocides (nematicides) is one of the alternatives, but this must be performed before any symptoms occur and is labor consuming. Research is now being conducted on the possibility of breeding resistant pines, as different

degrees of resistance can be observed among various strains of pine trees.

FWW: Mainly insecticides have been used against the FWW since its occurrence. Konno (1998) reported that FWW larvae had developed resistance to some insecticides

RWW: Farmers usually apply insecticide to nursery boxes before transplanting. The area treated covered 665,568 ha in 2000 which represented one-third of the paddy fields in Japan. No efficient natural enemies have been detected in either the USA or Japan. Two kinds of filamentous bacteria, which were introduced into rice fields, showed no appreciable effect on the RWW population (Hirai, 2000). Draining surface water for 2 weeks from paddy fields decreased the densities of the RWW (Shimohata & Kanoh, 1983). About 150 rice varieties originating in Japan or other countries were screened for tolerance to injury by this insect. A few varieties showed tolerance (Shaku *et al.*, 1984). However, those cultural control methods are mostly in an experimental phase.

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