

# 16

## Vector–Host Tree Relationships and the Abiotic Environment

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### 16.1 Introduction

Some cerambycid beetles of the genus *Monochamus* (Coleoptera: Cerambycidae) are known vectors of the pine wood nematode (PWN). These include *M. alternatus* in East Asia (Mamiya and Enda 1972; Morimoto and Iwasaki 1972; Lee et al. 1990; Yang 2004), *M. saltuarius* in Japan (Sato et al. 1987), *M. carolinensis* in North America (Linit et al. 1983), and *M. galloprovincialis* in Portugal (Sousa et al. 2001). Among these vectors, *M. alternatus* has been most intensively investigated, especially in Japan, because of its relatively long history and importance as a vector of the PWN. The purpose here is to review the literature focusing on the biology of *M. alternatus*.

*Monochamus* beetles are secondary insects that can attack only weakened or dying trees (Cesari et al. 2005). *Monochamus alternatus* is thought to have been a rare insect in Japan until the introduction of the PWN about 100 years ago. The life-history traits of *M. alternatus* acquired before the invasion of the PWN are, however, considered to be helpful in clarifying the outbreak and PWN epidemics (Togashi 2002, 2006b). Here an outline of the geographical distribution and life history of *M. alternatus* will be presented, followed by a discussion on the features of its food resources, weakened or dying host trees that strongly affect the development of the insect's life-history traits. As well, the effects of abiotic conditions on *M. alternatus* resource availability will be discussed in relation to the bionomics of the insect and pine wilt disease symptom development in host trees.

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## 16.2 Geographical Distribution of *Monochamus alternatus* and Other Vectors

*Monochamus alternatus* was originally described by Hope (1982) based on specimens from the Zhoushan islands in Eastern China (Zhejiang Province) (Makihara 1997). *Monochamus tesseraula* described by White (1858) is a synonym of *M. alternatus*. It occurs in Japan, Korea, Taiwan, continental China, northern Laos and northern Vietnam (Makihara 2004; Fig. III.1). In Japan, *M. alternatus* is present on three of the major islands, Honshu, Shikoku, and Kyushu, and small nearby islands, but the presence of *M. alternatus* in the northernmost area of Honshu before the pine wilt disease epidemic is questionable because the cool temperatures in those areas are unfavorable for the insects' oviposition and embryonic development (Takizawa 1982). In some of the isolated islands, such as Ogasawara, *M. alternatus*, accompanied by the PWN, is thought to have been introduced by human activity, that is, the transportation of contaminated wood material (Makihara and Enda 2005). Although PWN was introduced to Okinawa Island in southwestern Japan in 1973 (Kuniyoshi 1974), collection records of the 1940s indicate that *M. alternatus* is native to Okinawa (Makihara and Enda 2005). In Korea, *M. alternatus* was introduced to Pusan City probably from Japan and its range is expanding in the Korean Peninsula, although the insect is indigenous to Jeju-do Island (Makihara and Enda 2005). Though Makihara (2004) proposed dividing *M. alternatus* into two subspecies, the continental China-Taiwanese group and the Japan-Korean



**Fig. III.1** Geographical distribution of *Monochamus alternatus* (after Makihara 2004). Areas enclosed by dotted lines show the estimated natural distribution of *M. alternatus*. Solid squares indicate population spread by human activities

group, based on different morphological features, the two groups are not genetically distinct from one another (Kawai et al. 2006).

*Monochamus saltuarius* has been found in Finland, northern Italy, Russia, north-eastern China, Korea, Sakhalin, and Japan, suggesting a wide distribution across Eurasia. In Japan, its distribution is considered to be rather restricted to the cool summer areas in Honshu, Shikoku and a part of Kyushu, but not in the northernmost part of Honshu and Hokkaido (Makihara 1997). *Monochamus galloprovincialis* is widely distributed in Eurasia through North Africa, but not in Japan (Makihara and Enda 2005). The distribution of *M. carolinensis* is restricted to North America. It has been collected from southeastern Canada through Mexico, including the east coast and mid-western USA.

## 16.3 Life History of *Monochamus alternatus*

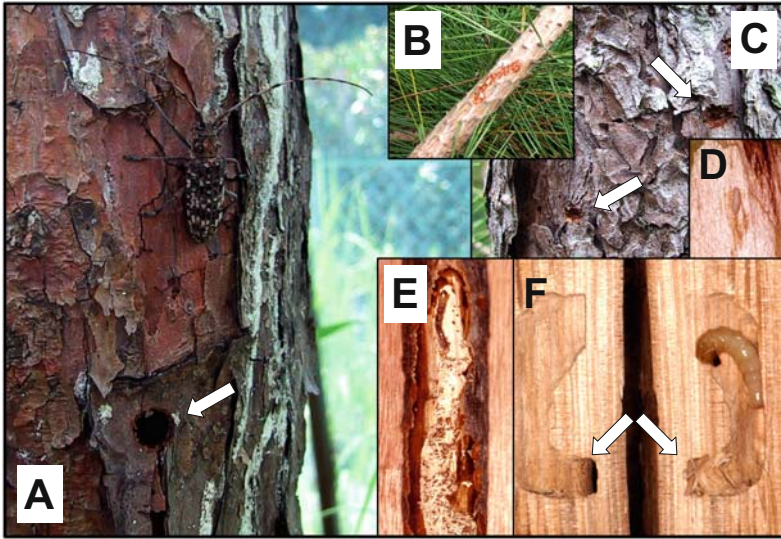
### 16.3.1 Adult Emergence and Flight Season

*Monochamus alternatus* has 1- and 2-year life cycles in Japan (Kishi 1995) where adults emerge from dead host trees once a year, in late spring through summer. The emergence period differs among locations; early April through August in Okinawa in the southwestern islands (Irei et al. 2004), May through July (Togashi and Magira 1981) or May through August (Kishi 1995) in central Japan, and late June to August in northern Honshu (Chida and Sato 1981; Hoshizaki et al. 2005). In southern China, *M. alternatus* has two to three generations per year, thus, the seasonal change in the number of emerging adults shows two to three peaks between April and November (Song et al. 1991).

The mean longevity of male and female adults is 70.1 and 65.9 days, respectively, in outdoor cages, and this decreases as they emerge later (Togashi and Magira 1981). In the laboratory, mated female adults originating from Taiwan show an average longevity of 179.7 days, which is shorter than that of unmated females (Zhang and Linit 1998). The mean longevity of *M. alternatus* adults is longer than that of *M. saltuarius* (57.3 days for fertile females; Jikumaru et al. 1994), *M. carolinensis* (103.4 days for mated females; Zhang and Linit 1998) and *M. galloprovincialis* (64.0 days for mated females; Naves et al. 2006c) reared in the laboratory. In central Japan, *M. alternatus* adults occur in early June through late September in the field (Shibata 1981; Togashi 1988). The flight season on Okinawa Island starts in April and lasts through October or November (Nakamura et al. 2005).

### 16.3.2 Adult Activities and Fecundity

*Monochamus alternatus* adults are reproductively immature at emergence. They feed on the bark of pine twigs or other conifers for survival and sexual maturation (Fig. III.2). This is often referred to as “maturation feeding”. The pre-oviposition



**Fig. III.2** Life cycle of *Monochamus alternatus*. **A** female adult coming out of an emergence hole (arrow), **B** feeding wounds by adult beetles on a *Pinus thunbergii* twig, **C** oviposition scars (indicated by the arrows), **D** an egg laid in the inner bark, **E** a feeding larva and frass under the bark, **F** a mature larva in a pupal chamber (arrows show the entrance hole) (see Color Plates)

period is 16–30 days (Enda and Nobuchi 1970), although the first egg deposition has been recorded as early as 6 days after emergence in a warm area (Ido and Takeda 1974) and as late as 61 days in a cool area (Takizawa 1982). The development rate of the female's ovary is affected by the quality of food: Ovary development is faster for females provided with current-year twigs of *Pinus densiflora* than those provided with 1- or 2-year-old twigs (Katsuyama et al. 1989). Males need about 5 days after emergence to inseminate females (Nobuchi 1976). Feeding response is elicited by extract of pine twig bark (Miyazaki et al. 1974) and is inhibited by ethane and other chemical components of pine needles (Sumimoto et al. 1975).

Immature adults randomly disperse by flying (Togashi 1990c) whereas mature adults are strongly attracted to volatiles emitted from dying or newly killed trees (Ikeda and Oda 1980; Ikeda et al. 1980b, 1981), and as a result are concentrated around such trees (Shibata 1986; Togashi 1989b). On those trees, they mate, and oviposit. A tethered flight experiment indicated that reproductively immature adults have higher flight activity than mature adults (Ito 1982), and the laboratory result was supported by a mark-and-recapture study in the field (Togashi 1990b). Adults move by walking or short-range flights in the pine canopy, where the distance traversed is estimated to be 7–40 m week<sup>-1</sup> (Togashi 1990c) or 10.6–12.3 m during

their lifetime (Shibata 1986). The beetles sometimes disperse over a long distance. A laboratory experiment with a flight mill recorded a maximum distance of 3.3 km or a maximum duration of 58 min of continuous flight (Enda 1985). Under field conditions, a released adult was recaptured 2.4 km away from the release point 4 days later (Ido et al. 1975). Wild adults flew over the sea to bait pine logs set on pine-free islands, showing a flight of at least 3.3 km from the nearest pine forest infested with *M. alternatus* (Kawabata 1979). These results demonstrate that *M. alternatus* adults can disperse over long distances of 2–3 km by flight, though such dispersal may be infrequent. A mathematical model indicated that long-distance dispersal of *M. alternatus* contributes greatly to the spread of pine wilt disease (Takasu et al. 2000).

Both males and females are attracted to the volatiles of the weakened host trees (Ikeda et al. 1980a,b), which likely helps them find a mating partner. Males have a volatile pheromone to attract females and both sexes have a contact pheromone on the body surface that elicits copulatory behavior in males (Kim et al. 1992). Thus, in mating, males are initially passive, just waiting for a female, and when a female touches his body, he dashes forward and mounts her (Fauziah et al. 1987). They form a long period of pair bond (23–390 min) and copulate repeatedly even after the female starts oviposition (Fauziah et al. 1987). Adults of both sexes copulate with several mates throughout their lifespan, suggesting that *M. alternatus* has a polygynous mating system (Fauziah et al. 1987). In addition, a female adult can fertilize all eggs laid in her lifespan when inseminated once (Nobuchi 1976). Sperm removal behavior like short-time penis insertion (Yokoi 1989) was not observed for congeneric *M. saltuarius* (Kobayashi et al. 2003). Kishi (1995) suggested that pheromones emitted from *M. alternatus* adults of both sexes are dispersed over a wide range in the field, which has not been proven.

Larvae of *M. alternatus* can grow only in dying or newly killed pine trees, thus female adults try to find and lay their eggs on such trees. This is why adults are attracted to volatiles emitted from weakened trees. When ovipositing, the female adult makes a slit-like wound on the bark surface with her mandibles, then turns 180° to insert the ovipositor through the center of the wound into the inner bark (Nishimura 1973; Fig. III.2). When the outer bark is thick enough the oviposition site may appear as a cone-shaped pit. In most cases females deposit a single egg or no eggs in the inner bark through a wound; less frequently they lay two to three eggs. The mean number of eggs per oviposition scar (oviposition ratio) is about 0.5 (Ochi and Katagiri 1979; Togashi and Magira 1981). Oviposition is stimulated by some compounds present in the inner bark of pine trees (Islam et al. 1997; Sato et al. 1999a,b), and is inhibited by a jellylike secretion deposited by female adults on oviposition scars as well as larval frass (Anbutsu and Togashi 2001, 2002).

An age-specific fecundity curve ( $m_x$  curve) of female adults reared under outdoor conditions is unimodal (Togashi and Magira 1981). The mean lifetime fecundity of early emerged females (157.3 eggs) was greater than that of mid- and late-emerged females (78.0 and 23.5 eggs, respectively) (Togashi and Magira 1981). The mean lifetime fecundity of mated *M. alternatus* originating from Taiwan under laboratory conditions was 581.0 eggs (Zhang and Linit 1998), greater than that of

*M. saltuarius* (69.7; Jikumaru et al. 1994), *M. carolinensis* (451.3; Zhang and Linit 1998) and *M. galloprovincialis* (67.0; Naves et al. 2006c). Lifetime fecundity differs greatly among *M. alternatus* female adults and correlates positively with body size (Togashi 1997).

Oviposition scars show a clumped distribution among trees (Shibata 1984), because the number of oviposition scars per tree varies depending on the time when the trees are weakened (Togashi 1989b). A clumped distribution pattern of oviposition scars is also observed among parts of a tree trunk (Shibata 1984). Female adults tend to avoid parts of tree trunks with thick outer bark because it requires much time and energy to make an oviposition site (Nakamura et al. 1995a,b). As a result, more oviposition scars tend to be in the middle and upper parts of trunks (Yoshikawa 1987; Nakamura et al. 1995b). The number of oviposition scars in a unit area of the bark surface, however, shows a uniform distribution, probably resulting from deterrent oviposition at already-occupied sites by other eggs (Shibata 1984). The inhibitory effect of the jellylike secretion deposited in oviposition scars and larval frass on oviposition behavior may be responsible for this phenomenon (Anbutsu and Togashi 2001, 2002).

Adults are nocturnal (Nishimura 1973). Feeding is observed in the daytime as well as at night, while movement (flight and walking) and reproductive behavior (mating and oviposition) occur mostly at night (Nishimura 1973; Kichiya and Makihara 1991), although the beetles tend to be inactive from midnight through dawn, probably because of the low temperatures (Fauziah et al. 1987; Kichiya and Makihara 1991).

### 16.3.3 Development of Immatures

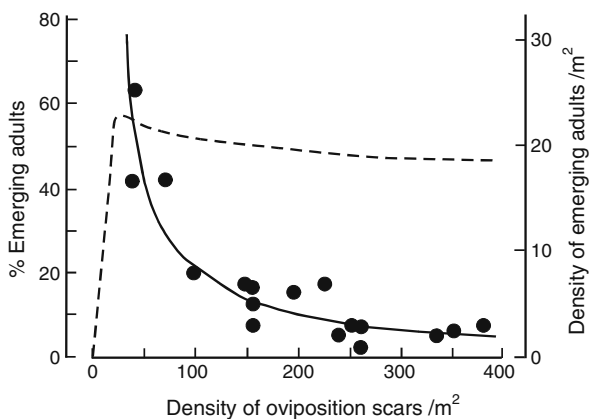
It takes 5 to 6 days for eggs to hatch (Ochi 1969). Hatchability decreases sharply when the daily average temperature is below 15°C (Takizawa 1982). Eggs are often killed by oleoresin from host trees (Togashi 1990a) that are weakened but probably maintain a low oleoresin exudation. Larvae grow by feeding on the inner bark and later partly on the sapwood. The larval gallery under the bark is packed with frass, which is a mixture of excreta and wooden fibrous shreds (Fig. III.2). Larvae under the bark make a clicking sound (Izumi and Okamoto 1990; Izumi et al. 1990), but the mechanism and function of this sound are unknown. *Monochamus sutor* larvae seem to make a sound by scratching the bark with their mandibles, and the sound could serve in protecting food resources from conspecific competitors (Victorsson and Wikars 1996). *Monochamus alternatus* larvae develop through four instars (Morimoto and Iwasaki 1974a; Yamane 1974a). Most fourth instar and some third instar larvae make tunnels in the xylem in late summer through autumn (Togashi 1989c), which have an oval-shaped entrance hole on the xylem surface and an elongated tunnel upward in the trunk (Fig. III.2). The terminal end of the tunnel usually curves toward the bark surface, thus the longitudinal section of the tunnel has a U-shape. Fully grown fourth-instar larvae make a pupal chamber at the

terminal end by packing wooden fibrous shreds toward the entrance hole, and overwinter there. Some larvae living under thick bark excavate depressions on the xylem surface and pupate there (Togashi 1980). The depth of the pupal chamber from the bark surface is mostly less than 10 mm, and tends to be deeper in cool areas (Kishi et al. 1982).

Pupation occurs after overwintering. The pupal stage lasts for 12–13 days at 25°C (Yamane 1974b). Newly eclosed adults require about 1 week for sclerotization. Sclerotized adults gnaw a round hole (ca. 1.0 mm in diameter) from the pupal chamber to the bark surface and exit to the outside (Fig. III.2).

### 16.3.4 Survival Rate of Immatures

The survival rate of *M. alternatus* in dead host trees, from egg to adult emergence, is as high as 28.9% (Ochi and Katagiri 1979) or 24.9% (Togashi 1990a; Table III.1). Key factor analysis shows that the third and fourth larval instars in the pupal chamber are the stages responsible for the fluctuation in the survival rate (Togashi 1990a). When the density of oviposition scars per unit area (approximately proportional to the egg density) of the bark surface increases, the density of emerging adults first increases and then saturates at a certain level (Morimoto and Mamiya 1977; Togashi 1986; Fig. III.3). This density-dependent process is materialized by deadly interference among the larvae and exploitative competition for food resources (Togashi 1986). Typically, the upper limit of the number of emerging adults is estimated to be about 20 per 1 m<sup>2</sup> bark surface (Morimoto and Mamiya 1977). *Monochamus alternatus* has many natural enemies such as entomogenous microorganisms, parasitoids, predatory insects, and woodpeckers (Table III.2). Natural enemies such as insect predators and parasitoids are density-independent mortality factors (Togashi 1986). Some natural enemies including the insect pathogenic



**Fig. III.3** Relationship between densities of oviposition scars and emerging adults of *Monochamus alternatus* per 1 m<sup>2</sup> on the surface of the bark on pine logs (reproduced from Morimoto and Mamiya 1977, with permission). Solid and dotted line show the trends in the percentage of emerging adults to the number of oviposition scars and number of emerging adults, respectively

**Table III.1** Life tables of *Monochamus alternatus* within dead *Pinus thunbergii* trees in Ishikawa, central Japan (Togashi 1990a)

Age class (x)	1980-1981 generation			1981-1982 generation			1982-1983 generation			1983-1984 generation			1980-1984 generations											
	$l_x$	$100q_x$	$d_x$	$l_A$	$l_B$	$l_c$	$100q_x$	$d_x$	$l_A$	$l_B$	$l_c$	$100q_x$	$d_x$	$l_A$	$l_B$	$l_c$	$100q_x$	$d_x$	$l_A$	$l_B$	$l_c$			
Egg	1,000.0	5.2	6			1,000.0	0.5	1			1,000.0	3.1	3			1,000.0	0.0	0			1,000.0	2.2	10	
Resin		28.7	33				17.9	34				18.8	18				31.0	18					22.4	103
Unknown																								
Total	660.9	33.9	39	76	6	815.8	18.4	35	155	0	781.2	21.9	21	75	0	689.7	31.0	18	40	0	753.8	24.6	113	346
Bird predation		0.0	0				0.0	0				0.0	0				2.5	1					0.3	1
Unknown		7.8	4				7.9	10				16.9	13				17.5	7					11.5	34
Total	609.0	7.8	4	47	18	751.6	7.9	10	117	28	649.4	16.9	13	64	7	551.7	20.0	8	32	0	664.4	11.9	35	260
$L_{5,4}$ (Before completion of PC)		4.2	3				0.8	1				1.3	1				5.6	1					2.0	6
Conspecific bites		0.0	0				1.6	2				2.6	2				0.0	0					1.4	4
<i>A. initiator</i>		0.0	0				0.0	0				1.3	1				11.1	2					1.0	3
Insect predation		0.0	0				1.6	2				0.0	0				5.6	1					1.0	3
Bird predation		11.1	8				15.9	20				31.2	24				11.1	2					18.4	54
Unknown		15.3	11	61	17	602.4	19.8	25	101	68	413.2	36.4	28	49	11	367.8	33.3	6	12	4	505.7	23.9	70	223
Total	516.0	1.2	1				1.0	4				0.8	1				0.0	0					0.9	6
Failure to pupate		0.0	0				0.3	1				0.0	0				0.0	0					0.1	1
Conspecific bites		9.4	8				3.8	15				7.5	10				3.7	3					5.2	36
Insect predation		42.4	36				10.6	42				7.5	10				23.7	19					15.4	107
Unknown		52.9	45	40	5	508.1	15.7	62	334	27	348.0	15.8	21	112	6	266.7	27.5	22	58	9	396.4	21.6	150	544
Total	242.8	0.0	0				0.5	1				0.0	0				2.6	1					0.6	2
Insect predation		9.4	3				4.0	8				4.2	3				12.6	5					5.6	19
Unknown		9.4	3	29	0	485.0	4.5	9	189	0	333.5	4.2	3	69	0	225.6	15.4	6	33	0	372.0	6.2	21	320
Total	220.1	0.0	0				1.6	3				1.4	1				0.0	0					1.2	4
Failure to emerge		3.4	1				0.0	0				0.0	0				0.0	0					0.3	1
Insect predation		37.9	11				37.0	70				20.3	14				18.2	6					31.6	101
Unknown		41.4	12	17	0	297.7	38.6	73	116	0	216.0	21.7	15	54	0	184.6	18.2	6	27	0	248.7	33.1	106	
Total	129.0																							

$l_A$  shows the number of insects in more advanced age classes than the age class for estimation of mortality rate.  $l_B$  and  $d_x$  shows the numbers of live and dead insects in the age class concerned. Mortality rate ( $100q_x$ ) was calculated as  $\{d_x/(l_A + d_x)\} \times 100$ . PC in age class column represents pupal chamber in xy/lem. In causes of mortality, insect predation includes predation by *Trogassita japonica*, *Stenogostus umbratilis* and *Gonolabis marginalis*



**Table III.2** List of natural enemies of the pine sawyer beetle *Monochamus alternatus*

Category	Order: Family	Species	Stage(s) attacked	Literature
Entomogenous microorganisms				
		<i>Serratia marcescense</i>	L	e
		<i>Serratia</i> spp.	L	d, f
		<i>Beauveria bassiana</i>	L, P, A	d, e, f
Parasitoides				
	Hymenoptera			
	Braconidae			
		<i>Atanycolus initiator</i>	L	f
		<i>Spathius</i> sp.	L	f
		<i>Doryctus</i> sp.	L	e
		<i>Ecphylyus hattorii</i>	L	e
		<i>Iphiaulax impostor</i>	L	e
	Bethyliidae			
		<i>Sclerodermus</i>	L	f
		<i>nipponicus</i>		
		<i>Sclerodermus guani</i>	L	g
	Pteromalidae			
		<i>Cleonymus</i> sp.	L	f
	Ichneumonidae			
		<i>Dolichomitus</i> sp.	L	f
		<i>Megarhysa</i> sp.	L	e
	Coleoptera			
	Bothrideridae			
		<i>Dastarcus</i>	L, P, A	e
		<i>helophoroides</i>		
		<i>Dastarcus kurosawai</i>	L	h
	Diptera			
	Tachinidae			
		<i>Billaea</i> sp.	L	f
Insect predators				
	Hymenoptera			
	Formicidae			
		<i>Monomorium</i>	E	a, e
		<i>intrudens</i>		
	Coleoptera			
	Elateridae			
		<i>Stenagostus</i>	L	f
		<i>umbratilis</i>		
		<i>Paracalais berus</i>	L	e
		<i>Paracalais larvatus</i>	L	h
	Histeridae			
		<i>Platysoma lineicollis</i>	L	e
	Rhizophagidae			
		<i>Mimemodes</i>	E	e
		<i>emmerichi</i>		
		<i>Rhizophagus</i> sp.	E	f
	Trogossitidae			
		<i>Trogossita japonica</i>	L, P, A	a, e
	Cleridae			
		<i>Thanasimus lewisi</i>	L	a, e
	Hemiptera			
	Reduviidae			
		<i>Velinus nodipes</i>	A	e
	Neuroptera			
	Inoceliidae			
		<i>Inocellia japonica</i>	L	e
	Dermaptera			
	Anisolabididae			
		<i>Anisolabella</i>	L	f
		<i>marginalis</i>		
		unidentified	L	e
Chilopoda				
	Scolopendromorpha			
		unidentified	L	e

(continued)

**Table III.2** (Continued)

Category	Order: Family	Species	Stage(s) attacked	Literature
Arachnida	(Spiders)		A	b
Woodpecker	Piciformes Picidae	<i>Dendrocopos major</i>	L	c

*E* eggs, *L* larvae, *P* pupae, *A* adults

a: Ochi and Katagiri (1979)

b: Morimoto and Mamiya (1977)

c: Igarashi (1980)

d: Katagiri and Shimazu (1980)

e: Taketsune (1983)

f: Togashi (1989c)

g: Zhang and Song (1991)

h: C. Kiyuuna (personal communication)

fungus, *Beauveria bassiana* (Okitsu et al. 2000; Shimazu and Sato 2003), parasitoid insects such as *Sclerodermus guani* (Zhang and Song 1991) and *Dastarcus helophoroides* (Urano 2004), and the Great Spotted Woodpecker, *Picoides major* (Yui et al. 1993) have been intensely studied for the use in controlling *M. alternatus*.

*Monochamus alternatus* immatures can be reared aseptically on an artificial diet containing sliced or minced host tree tissue (Kosaka and Ogura 1990).

## 16.4 Predictability of Food Resources for *Monochamus alternatus*

Togashi (2002, 2006a) pointed out the spatio-temporal unpredictability of food resources for *M. alternatus* larvae before the invasion of Japan by PWN unlike the adults. He also pointed out that the life-history traits of *M. alternatus*, such as a long adult flight season due to long adult longevity and 1- and 2-year life cycles, are adapted to the unpredictable larval food resources. He then related the life-history traits to the pine wilt disease epidemic. Here his views are outlined along with additional novel information.

### 16.4.1 Before PWN Introduction

*Monochamus alternatus* adults fed on the bark of twigs of healthy or weakened pine trees. In general, pine twigs in a pine stands are abundant and considered not to be limited food resources regardless of their long life span. In addition,

the adults can feed on various species of the genus *Pinus* (Furuno and Uenaka 1979) or non-pine conifers such as trees of the family Pinaceae, Japanese cedar (*Cryptomeria japonica*) and cypress (*Chamaecyparis obtusa*) (Yamane and Akimoto 1974; Nakamura and Okochi 2002). This flexibility of food selection may be helpful for adults lacking pine trees to survive until they find a new safe site after wandering around. Consequently, food shortage rarely occurs for *M. alternatus* adults.

On the other hand, *M. alternatus* larvae feed on the inner bark of weakened or newly killed trees in the family Pinaceae, especially the genus *Pinus* (Table III.3). They can not survive in live host trees because of oleoresin, the main defense agent

**Table III.3** List of trees species on which *Monochamus alternatus* larvae live

Genera	Species	Literature
<i>Pinus</i>	<i>armandii</i> var. <i>amamiana</i>	f
	<i>banksiana</i>	a, b
	<i>densiflora</i>	a, b
	<i>elliottii</i>	a, c
	<i>engelmannii</i>	c
	<i>greggii</i>	c
	<i>khasya</i>	c
	<i>koraiensis</i>	a
	<i>leiophylla</i>	c
	<i>luchuensis</i>	a, b
	<i>massoniana</i>	a, c
	<i>nigra</i>	c
	<i>palustris</i>	c
	<i>palustris</i>	e
	<i>pinaster</i>	d
	<i>ponderosa</i>	c
	<i>pungens</i>	b
	<i>radiata</i>	c
	<i>strobus</i>	a, b
	<i>sylvestris</i>	c
<i>taeda</i>	b, c	
<i>thunbergii</i>	a, b	
<i>Abies</i>	<i>firma</i>	a, b
<i>Cedrus</i>	<i>deodara</i>	a, b
<i>Larix</i>	<i>kaempfer</i>	a
<i>Picea</i>	<i>abies</i>	a, b
	<i>jezoensis</i> var. <i>hondoensis</i>	a, b
	<i>morinda</i>	a, b

a: Kojima and Okabe (1960)

b: Kojima and Nakamura (1986)

c: Furuno (1972)

d: Mineo and Kontani (1973)

e: Kishi (1980)

f: Akiba et al. (2000)

in conifers. Trees that passed several months or more after death are also unsuitable for *M. alternatus* larvae because their inner bark is already occupied by other subcortical insects such as weevils and scolytids (Yoshikawa et al. 1986) or because the inner bark is completely exploited. Also, those trees may not satisfy the nutrition requirements for *M. alternatus* larval development. The occurrence of weakened or newly dead host trees are supposed to be relatively rare in pine forests unless pine wilt disease has spread. Although stressed pine trees resulting from shading by other trees constantly occurs in forest settings, the total amount is limited and not all trees are weakened during the flight season (Togashi 2006a). Many dead trees can be supplied by disasters such as forest fires, drought, wind and snow damage. Those events are, however, rare and quite unpredictable. We have pests and diseases of pine trees such as lepidopteran defoliators and *Armillaria* fungi, but these are usually not as devastating as pine wilt disease. Over all, we can regard food resources for *M. alternatus* larvae as rare or unpredictable, or both, in time and space, and this unpredictability of food resources should have worked as a strong determinant for *M. alternatus* to maintain the population (Togashi 2006a). In fact, it is said that *M. alternatus* was seldom captured before the pine wilt disease epidemic in Japan (Nawa 1937), suggesting that the unpredictability of food resource prevented their outbreak.

To utilize unpredictable food resources, *M. alternatus* seems to have refined its lifestyle. The long adult flight season (Shibata 1981; Togashi 1988) owing to long adult longevity (Togashi and Magira 1981; Zhang and Linit 1998) would increase the chance of encountering the few available weakened trees. The adults would reach host trees suitable for oviposition by their highly developed sensory system and flight ability. They have high reproductive potential (Ochi and Katagiri 1979; Togashi 1990a), so that they can surely produce offspring when they encounter scarce food resources. One- and 2-year life cycles within a population (mentioned later) lower the probability of extinction due to a lack of newly dead trees in a year (Togashi 2006b). Varying developmental times has a stabilizing effect on population density under unstable environmental conditions (Takahashi 1977).

### ***16.4.2 After PWN Introduction***

PWN is thought to have been introduced into Japan in the early 1900s (Mamiya 1983) from North America (de Guiran and Brugier 1989; Tarès et al. 1992a,b), whereas *M. alternatus* is indigenous to Japan. It can be inferred that the introduced nematode could easily establish a mutual relationship with *M. alternatus* once they co-occurred in a weakened tree, because they both originally had relationships with equivalent counterpart organisms of the same genus (i.e., North American *Monochamus* beetles such as *M. carolinensis* for the PWN, and the nematode *B. mucronatus* for *M. alternatus*). Unfortunately, the PWN is highly pathogenic to Japanese pine trees such as *P. densiflora* (Japanese red pine), *P. thunbergii*

(Japanese black pine) and *P. luchuensis* (Ryukyu pine). As a result, *M. alternatus* utilizes a massive number of weakened and dying trees killed by the PWN.

Epidemics of pine wilt disease caused by the PWN change the weakened pine trees from unpredictable to predictable resources. In central Japan, infection of the PWN on pine trees occurs only in the adult flight season of *M. alternatus*, primarily during summer, thus tree death resulting from nematode infection is mostly found in mid-summer through autumn (Togashi 1989b). In such a case, most newly killed trees are ready for oviposition of *M. alternatus*. The trees killed from pine wilt disease show contagious distribution probably because of the attractiveness of newly dead trees to reproductively mature *M. alternatus* adults (Togashi 1991b). Moreover, a positive, spatial correlation is observed between trees diseased the previous year and those diseased in the early season of the current year (Togashi 1991b). This may be caused by the latent infection of the PWN (Futai 2003a; see also Sect. 23.4) or transmission of the PWNs through grafted roots (Tanaka 2003). The occurrence of killed trees from pine wilt disease is predictable in time and space. In addition, the number of newly dead trees in PWN-infested pine stands is far greater than in uninfested forests. Yearly loss of pine trees often accounts for over 30% in PWN-infested stands and less than 10% in uninfested stands (Kishi 1995).

After the introduction of PWN, the occurrence pattern of newly dead pine trees that serve *M. alternatus* larvae as food resources changed completely. Life-history traits adapted to limited food resources for immature stages allow the prosperity of *M. alternatus* by using newly dead trees, and make it difficult for us to control pine wilt disease.

## 16.5 Temperature Effect on Development and Adult Prevalence of *Monochamus alternatus*

As an ectothermal organism, the development of *M. alternatus* is subject to ambient temperature. In Japan, *M. alternatus* has a 1-year life cycle (univoltine) when the larvae have adequate time for development at a suitable temperature. In areas with a short, cool summer, the larvae cannot complete their development within one season and thus have a 2-year life cycle (semivoltine) (Togashi 1986, 1989a,c). The two different life cycles are observed within a single *M. alternatus* population and the proportion of 1-year life cycles tends to decrease with an enhanced latitude or altitude with cooler summers (Kishi 1995). Japanese populations of *M. alternatus* have an obligate larval diapause (Togashi 1989a). Facultative diapause is observed in the southern part of the range (Enda and Kitajima 1990), resulting in two generations in a year (bivoltine) in Taiwan (Enda and Makihara 2006) and two or three generations in subtropical Guangdong Province, China (Song et al. 1991). In Okinawa, an island off southwestern Japan, the *M. alternatus* population is not bivoltine, and thus seems to have an obligate diapause, regardless of the subtropical climate (Kosaka et al. 2001a; Irei et al. 2004; Enda and Makihara 2006).

In winter, the first to fourth instar larvae of *M. alternatus* appear (Togashi 1989a). Some are in diapause and others are not. Diapause larvae are fourth instars with a yellowish white to yellow body and no food in the intestine. They enter diapause prior to winter and low temperatures in winter break the diapause (Togashi 1995). The diapause is terminated by mid-February in Ishikawa, central Japan (Togashi 1991c). Diapause larvae do not resume development even under suitable temperature conditions.

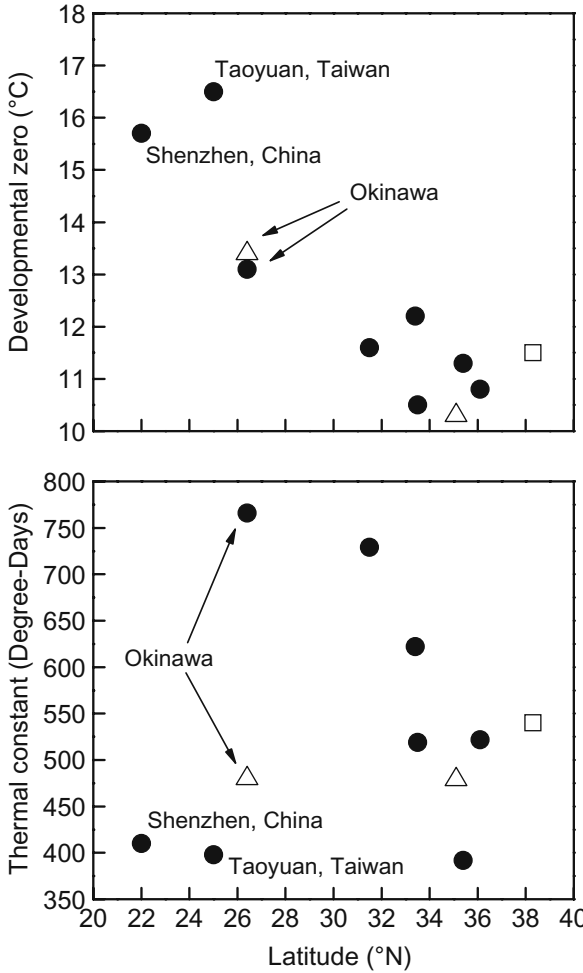
Pre-diapause third and fourth instar larvae skip the diapause when they experience low temperatures. They resume feeding in spring and become pupae and adults the following summer (Togashi 1989a,c, 1995). Larvae that overwinter as first and second instars resume feeding after winter and continue to grow. They enter the diapause as final instar before the second winter and terminate the diapause in the second winter; namely, those insects become semivoltine.

The development of post-diapause larvae to pupae and adults is subject to the thermal summation law. Thermal constant and developmental zero for post-diapause development has been estimated for *M. alternatus* populations originating from different locations in Japan as well as Taiwan and South China (Igarashi 1977; Kosaka et al. 2001a; Enda and Makihara 2006; Fig. III.4). Developmental zero shows a latitudinal cline; it tends to increase as the latitude of places where *M. alternatus* populations were sampled decreased. This may indicate the adaptation of *M. alternatus* populations to local climate. In contrast, the thermal constant varies greatly among *M. alternatus* populations, although it is constantly low in populations with facultative diapause. The thermal constant for post-diapause development also shows great fluctuation from year to year even for a population in specified place (Fig. III.5).

Adult emergence of *M. alternatus* has been regarded as one of the most important pieces of information needed for determining the timing of spraying of insecticides for controlling pine wilt disease (Nakamura and Yoshida 2004; Yoshida 2006). Many efforts have been made to develop a prediction system for adult emergence time on the basis of thermal summation law, but they have not been fruitful. The uncertainty of the values mentioned above could be one reason. In addition, thermal conditions for immatures in dead pine trees subject to factors relating to the micro-habitat, for example, location of pupal chamber in the trunk (depth, sunny or shaded, etc.). Estimating the developmental zero and thermal constant for *M. alternatus* local populations is significant to better understand their life history, but is not sufficient to predict adult emergence time, especially under field conditions.

## 16.6 Different Availability of Host Trees in Different Locations

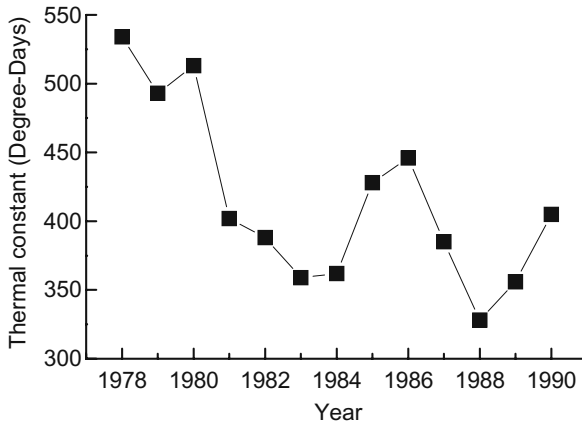
The occurrence pattern of weakened and newly killed trees, caused by pine wilt disease, changes in different locations, as does the adult emergence time (Fig. III.6). In general, high temperatures and low water content of the soil promote



**Fig. III.4** Cline of developmental zero (upper) and thermal constant of post-diapause development of *Monochamus alternatus*, which was calculated as the thermal sum required for 50% of adults to emerge. Different symbols represent data sources: squares Igarashi (1977), triangles Kosaka et al. (2001a), solid circles Enda and Makihara (2006)

disease development (Hotta et al. 1975; Suzuki and Kiyohara 1978). In central and south-western Japan, weakened and newly killed pine trees due to natural infection by the PWN occur mostly in early through mid-summer when hot temperatures and low precipitation prevail. The occurrence of weakened and newly dead trees coincides with the oviposition period of *M. alternatus*, resulting in a high proportion of dead trees infested with PWN and *M. alternatus* (Togashi 1989b).

In cool summer areas at high latitude or altitude, the emergence of *M. alternatus* adults starts in late June to July and ends in August (Chida and Sato 1981; Hoshizaki et al. 2005) resulting in a short flight season, thus, in such areas, PWN transmission is delayed. Moreover, disease development itself is slowed by cool summer temperatures. Consequently, a substantial proportion of diseased trees develop

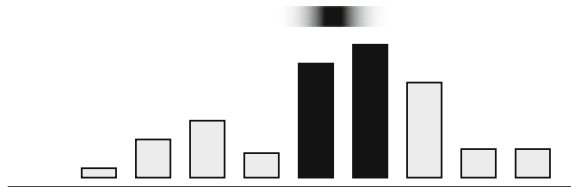


**Fig. III.5** Yearly fluctuation in the thermal constant of post-diapause development of *Monochamus alternatus* at Forestry and Forest Products Research Institute at Tsukuba, Ibaraki (Data from Enda 2006). Adult emergence from trees killed from pine wilt disease in the field was recorded every year. The thermal constant was calculated as the thermal sum required for 50% of the adults to emerge using daily average temperatures from meteorological data assuming a developmental zero of 11°C

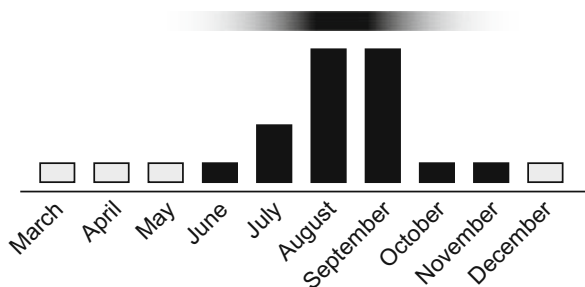
Central Japan



Northeastern Honshu (cool summer area)



Okinawa (subtropical area)



**Fig. III.6** Temporal relationships between the prevalence of newly killed pine trees, caused by pine wilt disease, and the oviposition season of *Monochamus alternatus* in different localities. The vertical bars indicate the relative abundance of newly killed trees. The oviposition season of the insects in each location is represented by the horizontal bar on each graph, in which dark shading shows a high oviposition activity. Newly killed trees occurring during the oviposition season are infested with *M. alternatus* (solid) and the others are not infested (gray)



symptoms after autumn. Chlorosis does not progress in winter because of the suppression of symptom development under low temperatures; it resumes in spring when temperatures rise sufficiently. Asynchronism between the oviposition period and tree mortality lowers the proportion of dead trees infested with *M. alternatus*; however, some newly dead trees in the year after PWN infection are used by *M. alternatus* for oviposition.

In the subtropical climate of Okinawa, pine wilt symptom development progresses even in winter, though the occurrence of newly dead trees has a distinct peak in June to July (Nakamura et al. 2005). The flight season of *M. alternatus* in Okinawa is as long as April through November, but they still can not utilize newly dead trees occurring in winter and early spring. As a result, we can find a numerous dead pine trees without *M. alternatus*, unlike the situation in central Japan with a moderate climate.

Pine wilt disease provides food resources to *M. alternatus*, while the temporal pattern of the occurrence of diseased trees varies owing to different climates and the flight seasons of adult insects, thus, we can conclude that the availability of diseased trees to *M. alternatus* differs depending on the biotic and abiotic conditions relating to pine trees, PWN and vector insects. It seems that the conditions occurring in central and southwestern Japan facilitate the efficient propagation of *M. alternatus* and pine wilt disease epidemics.

## 16.7 Concluding Remarks

*Monochamus alternatus* is a secondary insect that attacks only weakened or dying host trees, like other *Monochamus* species (Cesari et al. 2005). To utilize such rare and unpredictable resources, secondary insects should have the life-history traits shown in *M. alternatus*, at least to some extent (Togashi 2006b). Most of them, however, could not cause serious damage such as the mass mortality of trees, merely provoking problems in the wood production process, such as deterioration of wood quality by boring holes or staining, when the trees are stressed or killed by natural disasters or forestry operations. Some scolytid species associated with pathogenic fungi change from secondary to primary pests by mass attack at high population levels (Paine et al. 1997). *Monochamus alternatus* does not need mass attack to kill a pine tree because of the extreme pathogenicity of PWN to susceptible host trees. They seem to have changed from secondary to primary pests just by establishing a relationship with an alien pathogen introduced by humans. The prosperity of *M. alternatus* accompanied by the PWN must be recognized as an exceptional case of biological interaction.

*Monochamus alternatus* is widely distributed from subtropical to cooltemperate areas (Fig. III.1) and PWN has already spread throughout much of this area. There is considerable difference in the levels of environmental factors among the areas, and such differences are reflected in the development of *M. alternatus*, symptom

development in host trees and their interactions (Fig. III.6). Moreover, there are at least two geographically separate groups showing facultative and obligate diapause (Enda and Makihara 2006). We must take into account local differences in the bionomics of the vectors and host response to better understand the epidemic and make a control system against pine wilt disease.