15 Introduction

Soon after *Bursaphelenchus xylophilus* (pine wood nematode, PWN) was shown to be the causative agent of pine wilt in Japan a pine sawyer beetle, *Monochamus alternatus,* was identified as its vector (Mamiya and Enda 1972; Morimoto and Iwasaki 1972). Later, in the USA, *M. carolinensis* was recognized as the primary vector of the PWN (Kondo et al. 1982; Wingfield and Blanchette 1983). Following these discoveries biological studies began on *M. alternatus* and *M. carolinensis*.

Chapter 16 mainly reviews the biology of *M. alternatus*, which occurs in East Asia from Japan to northern Vietnam and Laos. Thus, there is a great variation in the life cycle; a 1- or 2-year life cycle in Japan and two or three generations a year cycle in subtropical China. Different life cycles are controlled by the insect's obligate or facultative larval diapause. After terminating diapause in winter, the larvae resume their development at temperatures above a lower limit (developmental zero). Chapter 16 summarizes the latitudinal cline in developmental zero of post-diapause development and the difference in the thermal constant among local populations. The author discusses the temporal relationship between seasonal occurrence of newly killed (from pine wilt disease) host trees and oviposition of *M. alternatus* in different localities to understand the differences in pine wilt disease epidemiology.

This part also reviews life-history traits of *M. alternatus* such as adult longevity, fecundity, flight performance, spatial distribution of immature stages, larval cannibalism, sound production, and key stages responsible for the survival rate of the immature stage. Chemicals affect adult behavior; for example, (1) acetone extracts from 1-year-old twigs of *Pinus thunbergii* elicit a strong feeding response from adult beetles, (2) ethane and saturated hydrocarbons with straight C_5–C_{10} chains that are contained in *P. densiflora* foliage show a strong feeding repellent activity for adult beetles, (3) monoterpenes and ethanol emitted from dying and newly killed pine trees attract reproductively mature beetles, and (4) secretion from the spermathecal gland of beetle female deters the oviposition. Some of chemicals associated with the beetle's life history are introduced in Chap. 16. The prevalence of recently killed pine trees as larval food resources is considered to be one of the most important factors in determining the population growth of *M. alternatus*. Chapter 16 discusses the relationship between the life-history traits of *M. alternatus* and the different, seasonal occurrence patterns of newly killed pine trees before and after the PWN was introduced into Japan.

More knowledge is needed about PWN transmission biology before a complete understanding can be obtained regarding the pine wilt epidemic. Chapter 17 introduces the effect of PWNs on the longevity and flight performance of adult vector beetles. *Monochamus alternatus* adults with a heavy load of PWNs live for a shorter time than adults with a light load. A heavy PWN load reduces the flight performance of *M. carolinensis*; however, vector beetles with a heavy PWN load can induce pine wilt incidence on their own. Chapter 17 deals with the temporal pattern of PWNs transmitted per unit time from a beetle to pine twigs and the effects of temperature on PWN transmission. The PWN transmission curve of insect vectors changes from being L-shaped to unimodal in the early stages of a disease outbreak in a *P. densiflora* stand. This change is discussed in relation to the virulence-transmission association. This chapter does not deal with chemicals that are emitted from beetles and pine trees and which partly control the PWN's entry into and departure from beetles. This is reviewed in Chap. 13 of this book.

Chaper 17 also deals with the epidemiology of pine wilt disease. The spread pattern of PWN has so far been analyzed by modeling and analytical approaches. The spread pattern of the PWN within a pine stand is determined mainly by short-distance flight of the vector beetles relating to reproductive maturity, the effect of PWN load on the transmission pattern and beetle performance, and a positive, spatial correlation of wilt-diseased trees in two consecutive years. The spread pattern of PWN over pine stands is determined by the long-distance flight of beetles. The spread rate of PWN increases from zero with the increasing proportion of long-distance dispersers and abruptly reduces beyond a certain proportion due to the Allee effect. The spread of PWN over prefectures, Japanese administrative districts with a mean area of 8,038 km^2, is caused by humans transporting pine logs infested with PWNs and insect vectors. The mechanisms and rates of PWN spreading at various levels of spatial scales may be indicative for the control of pine wilt disease.

Insect vectors of the PWN are considered to have increased their range on a geological scale by flight. Now they can move by flight and transportation related to human activities. The genetic structure of a beetle population is made up by gene flow, mutation, genetic drift, and natural selection. The interactions among the PWN, beetle vectors, and trees in a pine stand are likely to change the respective ecological traits, resulting in the evolution of a pine wilt system. Thus, it is necessary to determine the genetical relationships between vector populations and those between beetles within a population. DNA markers are helpful tools to elucidate the genetic structure. Chapter 18 introduces molecular-ecology studies using two different resolution levels of DNA markers, mitochondrial DNA and microsatellite regions of nuclear DNA, to successfully represent the phylogenic relationship among *M. alternatus* populations in East Asia and the northward expansion pathways in the Tohoku district of Japan. Chapter 18 also describes a method for developing microsatellite markers.