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Summary

More than one million cubic meters of wood from *Pinus thunbergii* PARL. and *P. densiflora* SIEB. et ZUCC. have been annually destroyed by pine wilt disease since 1978 in Japan. This disease is caused by the pinewood nematode, *Bursaphelenchus xylophilus* (STEINER et BUHRER) NICKLE, which is vectored by a cerambycid, *Monochamus alternatus* HOPE. Various techniques have been developed and applied for disease control. Insecticide application for the adult vectors, especially aerial application, is the most effective among them, but it has been pointed out that the technique gives rise to various problems such as environmental pollution and destructive changes in pine forest ecosystem caused by insecticides. Thus, it is necessary to establish an integrated control program for this disease, which means an effective combination of various techniques, in order to decrease the number of insecticide applications. In the present study, both the population dynamics of *M. alternatus*, *B. xylophilus*, and *P. thunbergii* and the quantitative interrelations among the 3 species were analysed. The basic features of these interrelations were characterized in a 4-year study within a *P. thunbergii* stand at Oshimizu, Ishikawa Prefecture, including rearing and oviposition experiments of *M. alternatus* adults on *P. densiflora* logs. The mechanism of spread of the pine wilt disease within pine stands was deduced from the results of these studies. Based on these results, a simulation model describing the spread of pine wilt disease within a pine stand was constructed. Simulations were done with the model to evaluate the effects of 3 different control techniques and their combinations. Based on simulation results some proposals are presented on the control of the disease. The main biological aspects of the model are summarized as follows:

Biology of *M. alternatus*

1. *M. alternatus* required 1 or 2 years to complete its life cycle. A large proportion, 93 %, of individuals found within dead trees had a 1-year life cycle. They overwintered as 3rd or 4th larval instars. Some of them pupated without feeding after overwintering whereas the others resumed feeding and then pupated. Individuals with a 2-year life cycle overwintered as 1st or 2nd larval instars in the first winter and as 3rd or 4th larval instars in the second winter. The proportion of individuals with a 2-year life cycle was higher within dead trees weakened in September than within those weakened from June

through August. This is because oviposition time is closely correlated to development to occur before overwintering.

2. When the natural enemies and competitors were excluded, density dependent mortality occurred during a period from egg to adult emergence. A relation expressed by a saturated curve was observed between egg and emerging adult densities per unit bark surface of *P. densiflora* logs.
3. Identified factors responsible for mortality under natural conditions were conspecific larval killing by bites (intraspecific competition), failure in pupation and emergence, resin, 5 hymenopterous wasps (*Dolichomitus* sp., *Spathius* sp., *Atanycolus initiator*, *Cleonymus* sp. and *Sclerodermus nipponicus*), a tachinid fly (*Billaea* sp.), 4 predacious insects (*Carcinophora marginalis*, *Trogossita japonica*, *Rhizophagus* sp. and *Stenagostus umbratilis*), a fungus (*Beauveria bassiana*) and a bacterium (*Serratia* sp.).
4. For the populations established within fresh, 1-m-long, *P. densiflora* logs, the survival rate from egg to adult emergence fluctuated from 0.355 to 0.566 over 3 consecutive years when they were placed in a seashore stand of *P. thunbergii* and it fluctuated from 0.374 to 0.547 when they were placed in a mountainous stand of *P. densiflora*. While for *P. thunbergii* trees killed by *B. xylophilus* in the other seashore pine stand, the survival rate fluctuated from 0.129 to 0.298 over 4 consecutive years when the populations lived within. The difference in survival rate between fresh logs and killed trees was caused by the difference in mortality mainly in the egg stage, the 3rd–4th larval instars, and the adult stage inside pupal chambers. The survival rate was closely related to the time of host tree decline: it was the smallest within dead trees weakened in June (0.15) and largest within those weakened in July (0.35). The fluctuation in total mortality to adult emergence, K , was governed primarily by the mortality in the 3rd and 4th larval instars in pupal chambers.
5. Using populations established within *P. densiflora* logs, life tables were constructed, for one year before the beginning of aerial insecticide (carbaryl) application, and for 2 years in each of which the insecticide was applied twice in June. In populations established by August oviposition, insect predation occurred in all years. In populations established by June–July oviposition, insect predation occurred in the year before application but did not occur in the 2 years with insecticide applications. Consequently, the mean survival rate was larger for populations established in June–July (0.87) than for those established in August (0.26) when insecticide was applied. A comparison of survival rates in the 3 different years, however, did not detect any effect of insecticide application.
6. Adults emerged from dead trees between June and July. Under normal meteorological conditions, the earlier the females emerged in the season, the larger their potential fecundity (Σm_x) became. Lower fecundity of females emerging late in the season

was partially caused by a higher proportion of sterile ones. The average fecundity ($\Sigma L_m x$) was 76–86 under normal meteorological conditions in 2 summers and 41 under rainy and cool conditions in the other summer. Consequently, the net reproduction rate (R_0) was estimated to be 9.1–10.3 under the former conditions and 4.9 under the latter conditions.

7. The average number of egg-laying slits per tree was largest on dead trees weakened in June–July (260–280 slits/tree) and it decreased as the time of tree decline was delayed. Oviposition ratio (number of eggs/egg-laying slit) did not vary with the time of tree decline. The estimates of emerging adults per tree was the largest on dead trees weakened in July (40 adults), followed by those on trees weakened in June (16 adults), August (10 adults), and September (4 adults).
8. In a pine stand, the adult beetles were present between June and September. The population density began to rise in early or mid-June. It peaked early in July, was constant for about 1 month, and was followed by a decrease in mid- or late August.
9. Adults showed an aggregated distribution within a pine stand. An analysis of the spatial relation between adults and weakened trees (including recently killed trees) indicated that early in the emergence period (in June) adults were distributed independent of weakened trees. From July onwards, they responded with greater aggregation on and near weakened trees, resulting in clumped distribution patterns. The spatial overlapping between adults and weakened trees became large when the quadrat size was 16–36 m². The seasonal change in their spatial relation was elucidated by the difference in the behavior of adults before and after reproductive maturation.
10. The dispersal of newly emerged adults was studied by a release-recapture analysis of INOUE (1978). The residence rate of adults on individual trees was large (0.56/week) when the stand canopy was closed and the adults dispersed randomly by walking and flying. In contrast, the residence rate was low (0.02–0.30/week) when the stand canopy was open. Adults under these conditions dispersed randomly by flight. The average distance traversed was estimated to be 7.1–37.8 m in the first week after emergence. The dispersal of adults just after emergence was affected by stand density, number of emerging adults, air temperature, and precipitation. The adults were also estimated to travel an average distance of 10–20 m per week, which was the weekly increment in the mean distance traversed by the adults which were recaptured within 50 m of release point during 3 weeks after the release.
11. The release and recapture of marked, laboratory-reared adults with known ages indicated that their activity increased until the 17th day after emergence and then decreased. The recapture rate per week of adults, which emerged from dead trees in the forest, was smaller in June or July (about 10 %) than in August or September (about 20%).

Population density fluctuation of *B. xylophilus* within pine trees

1. The temporal pattern in the population density of *B. xylophilus* within trees varied depending on the time of tree decline. In November or December, there was no significant difference in the *B. xylophilus* densities among trees weakened in any month from June to September (100–200 nematodes/gram dry wood). On the contrary, the density was significantly smaller for the populations within trees weakened in October (0.3–2.1 nematodes/gram dry wood).

Interrelation between *M. alternatus* adults and *B. xylophilus*

1. The average number of *B. xylophilus* within *M. alternatus* adults decreased as the season advanced.
2. The number of *B. xylophilus* within *M. alternatus* adults varied from 0 to 150,000 just after adult beetle emergence. Nematode density in beetles was significantly affected by the *B. xylophilus* density within trees in November–December as well as the water content of xylem.
3. A drastic reduction of *B. xylophilus* in *M. alternatus* adults occurred between the 10th and 40th day after beetle emergence. This period was not influenced by the initial number of *B. xylophilus* within *M. alternatus* adults.
4. The transmission curve of *B. xylophilus* by *M. alternatus* adults (temporal pattern in transmission of *B. xylophilus* from *M. alternatus* to pine trees) was unimodal in many cases whereas it was rarely L-shaped. The average transmission curves varied according to the class of the initial number of *B. xylophilus* within *M. alternatus* adults. In the case of beetles with more than 10,000 nematodes, the number of nematodes transmitted for 5 days began to rise from the 10th day after beetle emergence. It peaked during the period between the 15th and 25th day after beetle emergence (about 1,500 nematodes/5 days) and then it dropped abruptly. When the beetles carried 1,000–9,999 nematodes at emergence, a peak of their transmission curve occurred between the 25th and 40th day after beetle emergence (about 370 nematodes/5 days). In the case of beetles with 100–999 nematodes, their transmission curve peaked between the 15th and 25th day after emergence (38 nematodes/5 days). No peaks were obvious in the transmission curve of beetles carrying less than 100 nematodes.
5. The longevity of *M. alternatus* adults became shorter as the number of nematodes carried increased. Consequently, the percentage of nematodes remaining within a dead beetle had a tendency to increase as the initial number of nematodes carried increased.
6. A theory was presented on the influence of nematode on the reproduction of vector population, based on the results obtained in the present study: the initial number of nematodes within *M. alternatus* adults affected vector longevity, vector reproduction, and nematode transmission curve. Only a vector with more than 10,000 nematodes can

induce pine wilt disease. Diseased trees are suitable for vector oviposition, but these vectors with heavy nematode loads have a very short adult life span and do not contribute to population increase of the beetle. Vectors carrying 1,000 to 9,999 nematodes can cause the disease in healthy trees near weakened trees by aggregation for oviposition and copulation. The adult life span of these infected beetles is long enough to allow a significant contribution to beetle population increase. Vectors with less than 1,000 nematodes rarely induce disease even if they aggregate. Therefore they participate only in reproduction. These inferences suggest that nematode density in beetles divides the vector population into 3 functionally different groups, i.e., adults producing food for progeny, those reproducing, and those of intermediate character.

Spatio-temporal distribution of pine wilt diseased trees and their death process

1. A total of 168 trees were weakened from June through October for 4 years in a *P. thunbergii* stand composed of 249 trees. The number of newly weakened trees increased from June to August and then remained constant until October. A large percentage of them, 84 %, was killed by the following May. The remaining 16 % recovered oleoresin exudation early in the next season, but 64 % of these were killed in that season. When trees were weakened between June and October and were killed by the following May, their major mortality factor was concluded to be *B. xylophilus*, and minor factors were snow damage, intraspecific competition (suppression), and a complex of *Sirex nitobei* and *Amylostereum areolatum*. A total of 19 trees were killed between November and May although they were not judged to be weakened previously between June and October. The major mortality factor for these trees was concluded to be intraspecific competition.
2. In naturally *B. xylophilus* infected pine trees, nearly all foliage discolored during the year when trees were weakened or the following year. When tree decline was delayed, each stage of foliage discoloration, i.e. discoloration in a part of foliage, nearly all foliage, and all foliage into red-brown or brown, was also delayed. All foliage changed to red-brown or brown during either of the 2 periods, late August—late October or March—May irrelevant to the time of tree decline.
3. The weakened trees were distributed in clumped patterns in 1980 and 1981, during the early stages of infestation. In many cases they showed a double-clumped pattern. The degree of aggregation was larger in June or July than from August onwards in 1980 and 1981. In 1982 and 1983 they were uniformly distributed in June and July and in June. However, they showed a double-clumped pattern after August. The seasonal change in spatial distribution of weakened trees was ascribed to the occurrence of weakened trees after August near trees weakened in June or July.
4. The trees were frequently weakened in June or July when they were near the trees

weakened in the previous year even though all dead trees were removed from the study site before beetle emergence. Spatial overlapping between trees weakened in June—July of the current year and in the previous year was large at quadrat sizes of more than 25 m². It can be called aftereffect.

5. Based on the information and inferences obtained in the present study, it is concluded that 4 processes are related to the incidence of pine wilt disease. First, the disease may be induced via *M. alternatus* adults soon after emergence from dead trees. During a period of beetle emergence, many beetles may stay as a total on trees near dead trees from which they emerged because of a limited capacity of locomotion. Though each of them transmits only a few nematodes because of their young age, the neighboring trees may receive sufficient nematodes from the beetles to induce the disease. The incidence of disease by this process depends on the number of beetles emerging from dead trees and their dispersal rate.

Secondly, the disease may be induced via reproductively immature beetles after initial dispersal. They move around without being attracted by weakened trees, which is indicated by the beetle distribution in space independent of weakened trees. Trees may be infected via the beetles with numerous nematodes during this stage, because they can individually transmit enough nematodes to induce the disease. It may be these beetles which spread pine wilt disease in uninfested pine forests and thus these beetles may play an important role in the spread of this disease.

Thirdly, the disease may be caused by reproductively mature beetles. They aggregate on both diseased trees and neighboring ones for oviposition or mating. Since the beetles with numerous nematodes are short-lived, it is inferred that the aggregated beetles do not carry numerous nematodes at emergence. Some aggregated beetles carry a moderate number of nematodes at emergence and their transmission rate peaks on the 30th—35th days after emergence. Therefore, a contagious distribution of such beetles contributes to an occurrence of newly diseased trees near trees already diseased. This means that the diseased trees show a contagious distribution from August onwards independent of the infestation history of pine wilt disease in a forest. The nematode transmission rate by beetles which carry less than 1,000 nematodes is negligible and they are not associated with the incidence of pine wilt disease.

Fourthly, the disease may be induced by the aftereffect of heavy infestation, which means an increased incidence of the disease in June and July of the current year at the place where many trees were diseased in the previous year. When the diseased trees are not removed from a pine forest, this process as well as the first one may induce the pine wilt disease in trees near trees diseased in the previous year.

M. alternatus adults emerge from June through July and disappear late in September. Thus, it is considered that the 1st, 2nd, and 4th processes work simultaneously early in a

season. The relative significance of each process probably depends on the infestation history of a pine forest. The 3rd process may work primarily late in a season.

**Simulation model of the spread of pine wilt disease
within a pine stand and its control**

1. A simulation model of the spread of pine wilt disease was constructed using FORTRAN 77 language based on the results about the mechanism of spread of pine wilt disease summarized in here. The calculation showed that some diseased trees occurred in clumped distribution patterns when a small number of beetles with poor capacity of dispersal emerged. On the contrary, no diseased trees occurred when a small number of beetles with large capacity of dispersal emerged. But numerous beetles produced diseased trees which showed a random distribution pattern. Neither the initial number of beetles nor the stand size (number of trees in a stand) greatly affected the period of time required for over 80 % of the trees to be killed.
2. The effectiveness of manipulating different control techniques and their combinations was evaluated in the simulation. It was shown that control of the disease was obtained within 4 years when insecticide was applied for beetle adults twice at appropriate times or when insecticide was applied once along with more than 70 % immature beetle mortality using artificial techniques such as insecticide spraying, insecticide fumigation, and incineration of dead trees. But it was shown that control of the disease was difficult to obtain in a few years by only killing immature beetle stages. It was also shown that the planting of pine stands with disease resistant trees would be the most effective means of disease control. Even without perfect resistance to the disease, tree resistance magnified the effectiveness of other disease control techniques; for example, it enabled only one application of insecticide for beetle adults to lead to successful disease control in a few years.