

Review

Changes in Major Insect Pests of Pine Forests in Korea Over the Last 50 Years

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Abstract: Understanding the occurrence patterns of forest pests is fundamental for effective forest management from both economic and ecological perspectives. Here, we review the history of the occurrence patterns and causes of outbreaks and declines of pests in Korean pine forests over the last 50 years. During this period, the major pests of pine forests in Korea have shifted from pine caterpillar (*Dendrolimus spectabilis* Butler) to the pine needle gall midge (PNGM, *Thecodiplosis japonensis* (Uchida and Inouye)) and finally to pine wilt disease (PWD) caused by the pine wood nematode (*Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle). Outbreaks of pine caterpillar, a native species in Korea, have been recorded as far back as 900 years, and it was the most relevant forest pest in Korea until the 1970s. The decline of its importance has been attributed to reforestation and higher levels of subsequent natural enemy activity. The PNGM is an invasive species, first discovered in Korea in 1929, that became widely distributed by 1992 and the major forest pest in the 1980s and 1990s. A suite of parasitic wasps attacking the PNGM contributed at least partially to the decline of PNGM densities. Following the decline of the PNGM, damage from PWD has increased since 2003. These shifts in major forest pests might be related to changes in forest composition and interactions among forest pests. Therefore, a new management strategy for controlling forest pests is required to mitigate the decline of pine forests in Korea.

Keywords: invasive species; natural enemies; pine caterpillar; pine needle gall midge; pine wilt disease

1. Introduction

Understanding forest pest outbreaks is fundamental for the effective economic and ecological management of forest ecosystems. Outbreaks of forest pests are affected by both intrinsic and extrinsic factors. Intrinsic factors are related to the rate of population increase and cyclical population dynamics [1], while extrinsic factors include biological factors such as the interactions between species and the effects of abiotic factors such as temperature and precipitation [2]. Biological interactions include the bottom-up effects of forest composition and tree age and the top-down regulation exerted by natural enemies [2–4]. In addition, anthropogenic factors directly or indirectly influence forest pest dynamics [5]. Long-term monitoring data for pests and their analyses can allow us to understand

historical changes in natural forest ecosystems under the influence of both natural phenomenon and anthropogenic activities.

Long-term monitoring programs on forest pests allow us to describe abundance patterns of pests [6,7]. Schwerdtfeger [8] described population changes of three species of pine-needle feeding Lepidoptera (*Dendrolimus pini* L., *Hyloicus pinastri* L. and *Bupalus piniarius* L.) in a pine plantation in Germany between 1880 and 1940. Using these data, Turchin and Taylor [9] showed the periodical occurrence of these species. Meanwhile, Tenow [10] studied the outbreaks of *Oporina autumnata* and *Operophtera* sp. in the Swedish Scandes Mountains on the basis of historical data from 1862 to 1968, and periodic outbreaks of *Operophtera brumata* L. continued until the 1990s [11].

In Korea, the monitoring of forest pests has been conducted for both major and occasional pests such as *Thecodiplosis japonensis* (Uchida and Inouye) (pine needle gall midge (PNGM)) and *Hyphantria cunea* (Drury) (fall webworm) populations since 1968 [12], including the measurement of annual changes of densities, dispersal, and distributions [13]. Choi and Park [12] reported the occurrence and dispersal patterns of these invasive species with their ecology and management histories. However, few studies have examined the long-term changes in forest pest populations in relation to the conditions of the forest ecosystem.

Pine forests are one of the most important forests in Korea because of their dominance and cultural importance. Forests of *Pinus densiflora* Siebold and Zuccarini account for 26% of all Korean forests [14], and wood from *P. densiflora* has been intensively used in Korea since the Goryeo Dynasty (918–1392) [15]. The major forest pests in Korea have occurred in pine forests [12].

Here, we review the changes in the major pests of pine forests in Korea, in particular of stands of *P. densiflora*, over the last 50 years. We consider occurrence histories and ecologies of these pests as well as the environmental factors influencing the pests' population dynamics. Management strategies based on natural enemies and chemical controls are discussed and new directions for forest pest management are proposed.

2. Forest Change and Monitoring Records in Korea

Wood was the main building material in ancient Korea. Houses from different periods reflect the availability of wood for construction. Based on the materials used, Park and Lee [15] estimated that oak trees were the dominant material (57%) from 100 B.C. to 910 (Three Kingdoms Period of Korea), whereas pine trees were the dominant species from 910 to the 1910s (Goryeo and Joseon Dynasties) with increasing dominance from 71% in the early period to 88% in the late period [15]. The change in forests from oak to pine likely influenced the distribution and occurrence of animals living in the forests [16].

As the pine trees became dominant in Korean forests, the pine caterpillar (PC) (*Dendrolimus spectabilis* Butler) outbreaks were recorded in the Goryeo and Joseon dynasties. After the first record of a PC outbreak in *The History of Goryeo* (Goryeosa) in 1101 (<http://www.history.go.kr>), more than 50 cases of PC outbreaks were subsequently recorded in the history books of the Goryeo (918–1392) and Joseon (1392–1897) dynasties, such as *The History of Goryeo* (Goryeosa), *The Veritable Records of the Joseon Dynasty* (Joseon Wangjo Sillok, also called as *The Annals of the Chosun Dynasty*) and *Seungeongwon Ilgi* (<http://www.history.go.kr>). These historical records qualitatively describe both the occurrence and control of pests and the prevailing forest conditions, but they do so with little quantitative information.

Modern Korean forests are considered a successful example of reforestation, and the annual growing stock and species composition of forests have changed dramatically as a result [17] (Figure 1). After the Korean War in the early 1950s, deforestation was intensive, with the major causes of deforestation being utilization of wood as a fuel source and slash-and-burn agriculture [17]. In particular, Japanese red pines, *P. densiflora*, were intensively used for fuel from the 1950s to the early 1970s, with 10 million m³ of woods including pine woods consumed annually [18]. The area of slash-and-burn agriculture likewise increased until the early 1970s [19], when it was prohibited by the government new policy for reforestation, and the main domestic fuel sources were changed from wood to coal. Due to

this change in forest management policy, the growing stock in forests increased from 5.7 m³/ha in 1952 to 146.0 m³/ha in 2015 [14]. Meanwhile, the dominance of coniferous species decreased from 57.3% in 1970 to 41.8% in 2010 (Figure 1a), although *P. densiflora* remained the most dominant coniferous species, accounting for 60% of conifers [14].

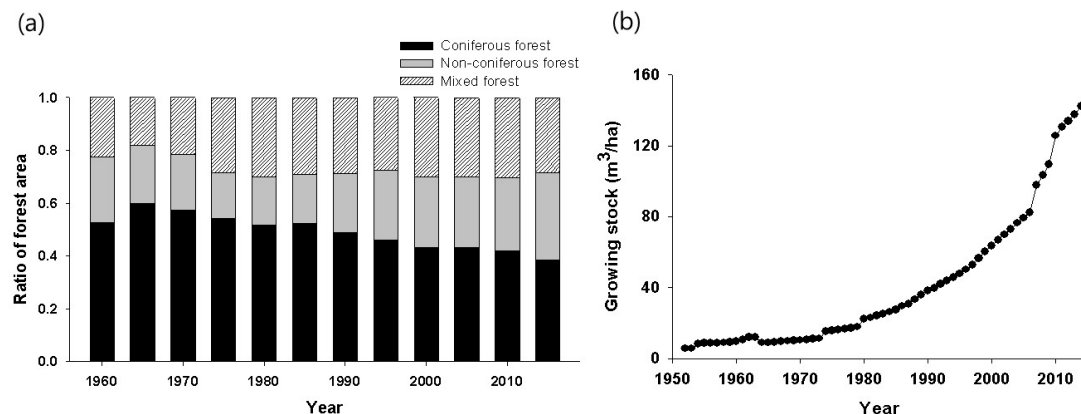


Figure 1. (a) Changes of forest composition in Korea from 1960 to 2015 and (b) annual changes in forest growing stock (m³/ha). The graphs were redrawn based on data from Statistical Yearbook of Forestry [14].

3. Monitoring of Korean Forest Pests

The Korea Forest Research Institute (later renamed the National Institute of Forest Science in 2015) initiated the Forest Insect Pests Monitoring Program in 1968. The occurrence of the PC, the major forest pests in 1960s, was checked annually at a series of national long term monitoring sites. The determination of the emergence period and leading edge of dispersal of the PNGM has been done since the mid-1970s. Outbreaks of occasional forest pests and the annual density of fall webworm (*H. cunea*) have also been monitored from the 1970s, and the areas damaged by black bast scale (*Matsucoccus matsumurae* (Kuwana)) and pine wilt disease (PWD) and their dispersal areas have been monitored since the 1980s. Monitoring data have been published in the form of annual reports entitled “Annual Report of Monitoring for Forest Insect Pests and Diseases in Korea” each year since 1968.

Targeted pests of the monitoring program have changed over the years according to the severity of each pest species. Major forest pests such as PWD, the PNGM, black pine bast scale, fall webworm, and Korean oak wilt disease caused by *Raffaelea quercus-mongolicae* (K.H. Kim, Y.J. Choi and H.D. Shin) and its insect vector (*Platypus koryoensis* (Murayama)) have been continuously monitored, although several domestic forest pests such as the PC were excluded in reorganization of monitoring system in 2016. Different factors have been monitored for different pests depending on their characteristics of damage. For PWD, dead pine trees at the forefront of PWD dispersal were sampled to determine if the trees were infected by the pine wood nematode; for the PNGM, the gall density per branch was used as a measure of PNGM density, and its parasitism was assessed by the microscopic observation parasitized larvae of the PNGM. The annual emergence patterns of forest insect pests such as the PNGM, fall webworm and the vector insects such as *Monochamus saltuarius* (Gebler), *Monochamus alternatus* Hope and *P. koryoensis* have been annually surveyed in at least nine sites since 2016. For occasional pests, the occurrence areas and degree of damages have been recorded. Recently, spotted lanternfly (*Lycorma delicatula* (White)), the citrus flatid plant hopper (*Metcalfa pruinose* (Say)) and ricanid plant hopper (*Ricania shantungensis* Chou and Lu) were observed in the field, and their damage areas have gradually increased [13,20].

The total forest area damaged by insect pests in South Korea has dramatically decreased from 421,234 ha in 1968 to 36,217 ha in 2016 (Figure 2). Such a sharp decrease was likely due to increases in both the budget and the manpower deployed to control forest insect pests. The area damaged by the

PC was the highest with 543,244 ha in 1965, from which it gradually decreased to less than 18,500 ha in 1983. Meanwhile, the area damaged by the PNGM was 390,185 ha in 1976 and gradually decreased to 73,206 ha in 2004. After that, the damaged area has increased up to 195,759 ha in 2006 and then decreased to 44,166 ha in 2016, showing annual fluctuations at different regions. These trends display that the PNGM is in the stabilization phase in terms of invasive species dispersal with the population dynamics. The area damaged by black pine bast scale was 5390 ha in 1984, and that area increased to 16,007 ha in 1996. It then gradually decreased to 4906 ha in 2016, indicating the saturation phase in its dispersal as well. Black pine bast scale occurs along the coastal areas where Japanese black pines grow, and the distribution of black pine bast scale has gradually increased [12]. Korean oak wilt disease was first observed in Korea in 2004, and the damage area increased to 4087 ha by 2008. Then the damaged area decreased with fluctuation to 2081 ha in 2016. The area damaged by PWD was 72 ha in 1988 and was less than 100 ha until 1999. However, it increased to 7811 ha in 2005, indicating rapid dispersal since 2000 [14]. The damaged areas increased up to 11,550 ha in 2013 and decreased to 6325 ha in 2016 due to intensive control measurements [14].

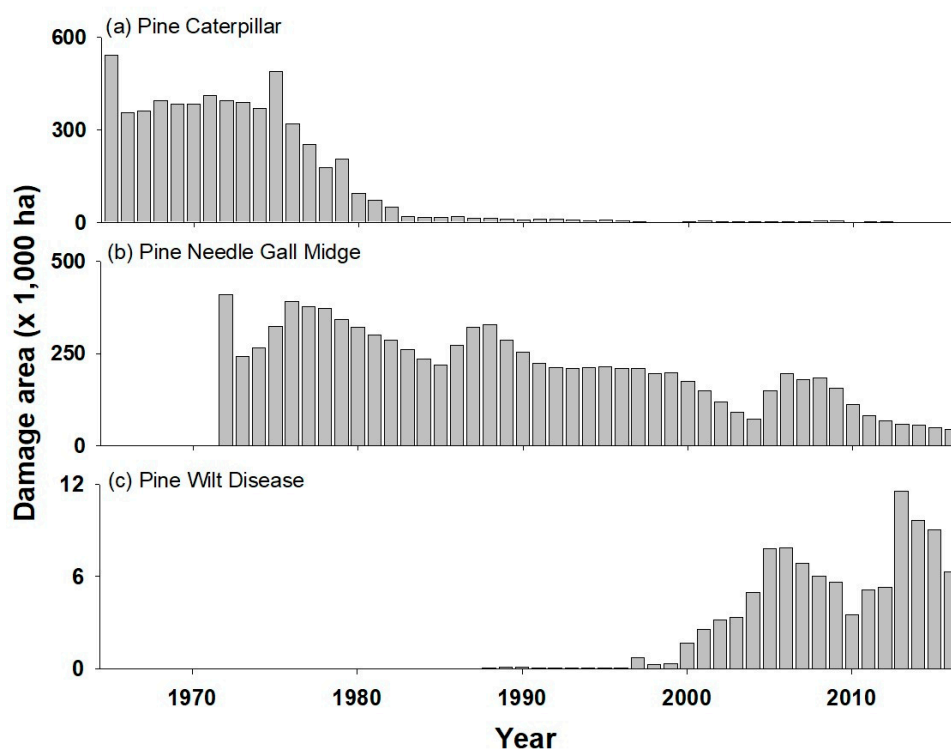


Figure 2. Changes of area damaged by forest pests in Korea. (a) Pine caterpillar, (b) pine needle gall midge, and (c) pine wilt disease. The graphs were redrawn based on data from Statistical Yearbook of Forestry [14].

It is worth noting that these three species have different impacts on pine trees and that the damaged area was not coincided with the number of dead trees. The defoliation of pine trees caused by the PC was rarely resulted in the death of trees, whereas pine trees infested by the PNGM displayed less than 30% of tree mortality in the outbreak area [21]. Meanwhile, pine trees infested by the PWD have mostly died [22]. Therefore, PWD has more serious impacts on forest ecosystems than other two species, although the overall damaged area is relatively smaller than others.

4. Changes in Major Pests in Pine Forests

During the last 50 years, the major forest pests in South Korea have been pine-feeding insects, and shifted from the PC via the PNGM to PWD. To understand these processes, we reviewed their ecologies and occurrence histories and the effects of environmental factors on the population dynamics

of these species. In addition, we considered management strategies with natural enemies and chemical controls. Following the review of Choi and Park [12] on the dispersal patterns of invasive species in Korean forests, we revised the occurrence and dispersal patterns of major insect pests in pine forests in South Korea.

4.1. Pine Caterpillar (PC)

4.1.1. Occurrence History and Ecology

The occurrence of the pine caterpillar (PC; *D. spectabilis*) had been documented in ancient literature, as well as in the pest monitoring reports. After its first recorded occurrence in 1101, the PC was documented in the Goryeo Dynasty and Joseon Dynasty (<http://www.history.go.kr>). PC outbreaks were also reported from the 1900s to 1950s. These records confirm that the PC has been a major forest pest in Korea for a very long time [23]. The PC is native in areas of the Asian Far East, such as Korea, China, Japan and Russia.

The PC was a major forest pest in Korea from 1950s to the early 1970s, after which its occurrence dramatically decreased to the point that it is now considered an occasional pest with very low abundance. Since 2000, the PC has occurred mainly in limited areas on islands or along roads rather than in forested areas [24]. The occurrence of the PC on islands has been reported consistently [13].

Before the 1970s, the PC was regarded as a univoltine species throughout South Korea, with no temporal or spatial variation [24–27]. However, the voltinism of the PC population in the central region of the Korean Peninsula was reported to have changed from univoltinism to bivoltinism in late 1990s and early 2000s [24,28]. Choi et al. [24] reported the host switching of the PC from the Japanese red pine to the pitch pine (*Pinus rigida* (Mill.)) by comparing with the results of Park and Kim [29], who noted a preference of the PC for *P. densiflora* over other pines, including *P. rigida* and *P. thunbergii*, under laboratory conditions in 1973.

The body length of PC adults is about 30 mm for males and 40 mm for females, with a wing span ranging from 50 to 67 mm in males and 64–88 mm in females [27]. Eggs are reddish brown and blue brown ovals, and their diameter is about 2 mm; larvae are dark yellow-grey with an irregular pattern of dark orange and light gray [27]. The life cycle of the PC was reported in detail by Choi et al. [24]. Pine trees heavily defoliated by the PC have typically died [27].

4.1.2. Environmental Factors and Management

The lower developmental temperature thresholds of the PC are 3.2 °C and 0.91 °C for eggs and larvae, respectively. The minimum and the optimal developmental temperatures for ≥4th instar PC larvae are 7.6 °C and 29.8 °C, respectively; for pupae, the minimum and optimal development temperatures are 12.5 °C and 30.4 °C, respectively [24].

Though the PC was a major forest pest in 1950s and 1960s, there were few studies on its population dynamics [30]. Hyun [30] reported that mortality of young larvae ranged from 70.9% to 93.4%, and precipitation in August was the main factor influencing larval mortality. Similarly, Kokubo [31] reported that precipitation was the main mortality factor in Japan for the younger larval stages, with mortality of the first and the second larval stages of 70%–80%.

Outbreaks of *Dendrolimus* spp. including *D. spectabilis* in Shandong province, China, have been found to be affected by drought [32]. Based on occurrence data for the PC from 1992 to 2012, outbreaks of the PC increased under drought conditions, and long-term or prolonged drought had a greater positive impact on PC outbreaks than short-term drought.

The egg mortality of the PC is caused mainly by parasitic wasps. In the late 1960s, the parasitism by *Trichogramma dendrolimi* Matsumura averaged 15.7%, while that by *Anastatus bifasciatus* (Geoffroy) was extremely low [30]. By 1999, the importance of these two egg parasitoids had reversed, with 0.01%–9.5% by *Trichogramma* sp. and *Anastatus* sp., while larval parasitism ranged from 1.6% to 22.8% for *Aleiodes dendrolimi* (Matsumura) and 8.0%–18.5% for an unidentified tachinid fly. Pupal parasitism

by the tachinid fly ranged from 13.5% to 41.3%, and PC populations have been found to be density-independently regulated by summer rainfall (especially in August) and parasitic insects [30,33].

Insect pathogens are also an important factor affecting PC abundance, often being the factor that terminates outbreaks, acting as a density-dependent source of mortality [30]. One such important pathogen has been the fungus *Beauveria bassiana* (Bals.) [34].

Suppression by natural enemies appears to have increased during over a period of reforestation. Generally, reforestation increase relative humidity, resulting in a presumably more favorable condition for insect-pathogenic fungi. For example, outbreaks of the gypsy moth in southern New England from 2015 to 2017 were attributed to unusual spring drought because activities of fungal pathogen, *Entomophaga maimaiga* Humber, Shimazu, and Soper were inhibited due to dry condition [35]. Reforestation may also promote increases in the populations of natural enemies such as parasitoids—both the number of species and their abundance—due to an increasing availability of alternative hosts [36,37].

Before the development of chemical pesticides and augmentative biological control methods, the manual collection of larvae by soldiers or citizens was employed, mainly during the Joseon Dynasty (1392–1897) (<http://www.history.go.kr>). Pesticides have also been widely used for the control of the PC [33], while in contrast, biological control using an egg parasitoid such as *T. dendrolimi* through the rearing and releasing the parasitoid was not attempted until the late 1990s and 2000s [33]. However, parasitoid releases were stopped around 2000 because of the decline of PC abundance.

4.2. Pine Needle Gall Midge (PNGM)

4.2.1. Occurrence History and Ecology

The invasive pine needle gall midge (PNGM) (*T. japonensis*) was a major forest insect pest in South Korea in the 1980s and 1990s, when it caused serious damage to *P. densiflora* and *P. thunbergii*. The first occurrence of the PNGM in Korea was reported in Seoul and Mokpo in 1929, possibly by two independent introductions. Meanwhile, the PNGM was first reported in Japan in 1901 without a report of the pest's origin [38].

After the first report of the occurrence in 1929, the PNGM spread to Busan (in the southern part of South Korea) in 1936 and to Danyang (in the middle part of South Korea) in 1964 [39]. By 1985, the PNGM occurred in more than 80% of South Korea and was found throughout the country by 1996 [40]. The dispersal of the PNGM in Korea was classified as Type 2 based on Shigesada et al. [41], moving at about 1.2–2.2 km/year during the early invasion phase [12] and accelerating to 5.2–8.2 km/year by the 1960s. For detailed information on the pest's dispersal in Korea, see Lee et al. [40] and Choi and Park [12].

The larvae of PNGMs overwinter in soil, and adults emerge from pupae in the soil from late May to early July [12]. Female adults lay eggs in the pine needles of pine trees, and larvae form galls at the bases of the pine needles, thus damaging their host pine trees through loss of new pine needles [42]. This results in a reduction of tree growth and an increase in tree mortality.

The PNGM reached outbreak levels five to seven years after invasion [43], and outbreaks have shown a periodicity of 10–12 years [44]. During outbreaks, the mortality of pine trees reached 30% [21] and then gradually decreased, probably due to increase in its parasitoids [27,45]. The area damaged by the PNGM was the highest (351,679 ha) in 1971 and then gradually decreased to 73,206 ha by 2004 [14]. This might have been caused by several factors such as PNGM management and the development of natural enemies [12,46].

4.2.2. Environmental Factors and Management

The minimum and optimal developmental temperatures for the PNGM are 5.9 °C and 27.0 °C, respectively, while the lower and the upper lethal threshold temperatures for post-diapause larvae through adults are 6.1 °C [47] and 30.0 °C [45], respectively. Soil water content in spring influences

PNGM density. The emergence rate increases with increasing soil water content, while it decreases with the decreasing water content [48]. A field life table analysis showed that population size was decreased due to a lower soil water content in spring [49]. This indicated that post-diapause mortality was a key factor to determine population size of the PNGM [12]. Choi et al. [50] determined the most influential environmental factors for population dynamics of the PNGM through spatial synchrony analysis using 20 years of monitoring data at 67 sites. They showed that differences in maximum temperature and precipitation were strongly related with variation in spatial synchrony, indicating that these density-independent factors potentially contributed to a fluctuation of the PNGM population.

Besides these abiotic environmental factors, population dynamics are also influenced by biological interactions such as competition, predator–prey, and host–parasite dynamics [51,52]. Park and Chung [42] developed models for the risk assessment of pine trees from the PNGM using two different artificial neural networks such as a self-organizing map and a multilayer perceptron, and they revealed that the crown density of pine trees highly influences the survival status of pine trees infested by the PNGM. Four species—*Inostemma matsutama* Yoshida and Hirashima, *Inostemma seoulis* Ko, *Inostemma hockpari* Ko and *Platygaster matsutama* Yoshida—parasitize the PNGM in Korea [53]. There are no studies on the origin of these species, although we infer that they co-invaded with their host. Of these, *I. seoulis* was first reported as a parasitoid of the PNGM by Ko [45], while *I. matsutama* and *P. matsutama* were later described by Yoshida and Hirashima [54]. Meanwhile, Ko [55] described *I. hockpari* as a new species in 1980. These species have different distribution patterns with different abundances [56]; *I. seoulis* and *P. matsutama* were widely distributed across Korea by 1985, while *I. matsutama* and *I. hockpari* displayed a relatively local distribution [56].

Parasitoids appear to play little role in the control of the PNGM in the early stages of its invasion of a new area, but the parasitoids become more important with time [52,53]. Two species, *I. seoulis* and *I. matsutama*, are the most common in the early phase of a PNGM invasion, while *P. matsutama* is found in the later, stabilized PNGM population [51]. During the invasive process or in the early stage of invasion, interspecific competitions between *I. matsutama* and *I. seoulis* and between *P. matsutama* and *I. seoulis* are minimal [53,57]. The interactions among three parasitoids are affected by differences in their phenology; *I. matsutama* and *I. seoulis* have different phenologies because of difference in their thermal biology [58], resulting in a weak direct competition. Choi et al. [51] reported that the differences in establishment sequence and competitive ability among the parasitoids in the invasion process of their host determined the parasitoid community's structure and dynamics.

Several methods were developed to manage the PNGM in South Korea, including trunk injection of insecticide, spray of insecticide on soil, silviculture, and the release of natural enemy [12]. The trunk injection of insecticide applied insecticides such as phosphamidon and acetamiprid to trunk of pine trees infested by the PNGM. This was effective but labor intensive and costly. Insecticides such as carbofuran and imidacloprid were sprayed on the soil where the PNGM occurred. Silviculture methods such as thinning were applied to reduce the tree mortality caused by the PNGM by improving the health of pine forests. The release of natural enemies such as parasitoids (*I. matsutama*, *I. seoulis*, *I. hockpari* and *P. matsutama*) was used to reduce the PNGM population level [12,56].

4.3. Pine Wilt Disease (PWD)

4.3.1. Occurrence History and Ecology

Pine wilt disease (PWD) caused by the pine wood nematode (PWN) (*Bursaphelenchus xylophilus* Nickle) is a serious pest for pine trees in many countries, including South Korea, Japan, China, Taiwan, and Portugal [12,46,59–61]. Pine trees in Asia and Europe are susceptible to the PWN, and the tree mortality of *P. densiflora* and *P. thunbergii* can reach 100% when infected by the PWN [12]. The PWN, originally from North America [62], is a tree-parasitic nematode with a body length ranging from 0.6–1.0 mm [63]. It develops to an adult through egg and 1st–4th juveniles. Specific dispersal juveniles dauer larvae enter the body of vectors such as *M. alternatus* and *M. saltuarius* through the tracheal

system when the vectors are larvae in the host tree. The female nematode, after mating, lays about 100 eggs.

PWD in South Korea was firstly reported at Mt. Geumjong in Busan in 1988 [12]. Its initial dispersal speed was relatively low at 1.1–1.2 km/year [64,65]. However, dispersal was accelerated to 13.8 km/year within 10 years [12]. These results show that the dispersal patterns of PWD are Type 2 based on Shigesada et al. [41]. Choi et al. [46] estimated the annual dispersal distance in South Korea to be 0.37 km, based on the annual changes of areas damaged by PWD in the early stages of invasion, and the annual dispersal distances were less than 1.0 km in most (88.8%) of damaged areas; they also showed that “jumping” was the dominant dispersal method in the early stages of the invasion, while later dispersal was due to the expansion of existing colonies. Dispersal speed increased with increasing human population density, suggesting human-mediated dispersal [66,67].

PWD damage occurred only on 72 ha in 1988 and less than 100 ha until 1999. Initially, the infested trees were removed to control PWD. A large number of infested pine trees (1598) were removed at Mt. Geumjong in 1989, and 14, 24, and 21 trees were removed in 1990, 1991 and 1992, respectively [13]. Meanwhile, 10, two and eight pine trees were cut to control PWD at outside of Mt. Geumjong in 1990, 1991, and 1992, respectively. These numbers indicate that PWD likely invaded Korea several years before the first report in 1988, and the initial control activities were not effective to minimize the dispersal of PWD in Korea because pine trees killed by PWD were found out of Mt. Geumjong within three years after the first report.

Meanwhile, the damaged area greatly increased to 7811 ha in 2005 [14], indicating that PWD had expanded its range significantly from 2000 to 2005 [12]. Nearly 1.7 million trees were cut to control PWD from May 2014 to April 2015, and the number of infected pine trees in 2017 decreased to 686,000 trees due to this intensive control effort [14].

The host plants of PWN in Korea include the Japanese red pine (*P. densiflora*), the Japanese black pine (*P. thunbergii*) and the Korean white pine (*Pinus koraiensis* Sieb. and Zucc.) [63]. The PWN vectors in Korea are *M. alternatus* and *M. saltuarius*, which both overwinter as larvae or pupae in a pupal chamber near the bark surface. Adults of *M. alternatus* emerge from late May to early August, and the female lays about 100 eggs [27], whereas adults of *M. saltuarius* emerge in mid-April to late May, earlier than *M. alternatus* [27,68]. PWN does not have the ability to disperse from an infected tree to a new tree outside of its vector. PWN individuals are transmitted from beetle vectors to pine trees during the maturation feeding of the adult beetles [12].

Togashi [69] evaluated the dispersal ability of *M. alternatus* by releasing 756 beetles, and 75.5% of them were captured within 100 m of the release point; it was estimated that *M. alternatus* could disperse 7.1–37.8 m per week in pine stands. The dispersal distances of *M. saltuarius* over its entire life span was estimated to be 2.71 and 1.93 km for males and females, respectively, based on a flight mill experiment [70]. The contributions of human-mediated dispersal of PWD were reported in China [71], Japan [72] and Korea [46,59]. Due to human-mediated dispersal, actual PWD dispersal distance was longer than the dispersal capacity of the vector insects.

4.3.2. Environmental Factors and Management

The development and distribution of PWD vectors are dependent on temperature with geographical variation. The lower threshold temperature for *M. alternatus* development in southern Japan and Taiwan is above 12 °C, whereas in northern Japan it is less than 13 °C [73]. The optimal development temperature of *M. saltuarius* is 20 °C, and the lower threshold temperature for development is estimated to be 10.1 °C for both sexes [74]. In Korea, the lower threshold, optimal, and upper threshold temperatures for post-diapause development of *M. saltuarius* are 8.3, 32.2 and 38.7 °C, respectively [75]. Park et al. [76] successfully predicted the spring emergence of *M. alternatus* based on a threshold temperature of 11.9 °C. These differences in lower threshold temperatures may explain the geographical distribution of two vectors in Korea. *M. saltuarius* is the most abundant in the central to northern areas of South Korea, while *M. alternatus* is found in the southern part of the country [68].

The transmission efficiency of PWN was increased when the nematodes and their vectors were exposed to temperatures in the range of 16 °C–25 °C [77], suggesting that optimal temperature positively affects the biological performance of both the nematodes and their vectors as well as their interactions.

The effect of temperature, precipitation and landscape features was evaluated on the level of risk of PWD occurrence [69]. A MB (*Monochamus/Bursaphelenchus*) index was developed [78] by summing the difference between the monthly average temperature and 15 °C when the monthly average temperatures exceeds 15 °C for one year [67]. The index displayed large differences between the PWD occurrence area in the field and the area predicted with the index in Korea, but the predictability of the index was improved by the modification of the threshold temperature [79]. Meanwhile, Park, Chung and Moon [22] developed a hazard rating model for pine trees and pine stands to PWD, showing that large trees have a higher risk rating than smaller ones because their high heights and a large crown volume induce a high probability to be exposure to vector beetles. They also revealed that pine stands at low altitude and south-facing slopes had high risk rating, thus indicating that the occurrence of PWD is highly associated with geographical factors.

Futai [80] demonstrated the importance of asymptomatic carrier trees in the spread of PWD. Meanwhile, Nguyen et al. [65] developed a spatial model to characterize the dispersal patterns of PWD in South Korea; they showed that asymptomatic carriers were important in the PWD dispersal and should be considered in the PDW management.

Information on the natural enemies of PWD vectors is limited even though there was over 30 years after the first occurrence of PWD in South Korea. A parasitic wasp, *Sclerodermus harmandi* (Buysson 1903), caused 54.7% and 98.6% parasitism in laboratory tests on larvae of *M. alternatus* and *M. saltuarius*, respectively [81]. Other reported natural enemies include the predator beetles *Temnochila japonica* Reitter and *Thanassimus lewisi* Jacobson and the parasitoids *Dolichomitus nakamurai* (Uchida 1928) and *Echthrus reluctator* L. [82]. In China, a total of 97 species of natural enemies have been reported, including 47 insects, 17 microorganism pathogens and 33 predatory birds [83]. Among these, four parasitoids [*Scleroderma guani* Xiao et Wu, *Scleroderma sichuanensis* Xiao, *Ontsira palliates* Cameron and *Dastarcus helophoroides* (Fairmaire)] and one predacious insect [*Cryptalaus berus* (Candeze)] have potential as biological control agents for *M. alternatus*. Generalist natural enemies that affect *Monochamus* populations require further study to assess their impact. Pathogenic fungi such as *Beauveria brongniartii* (Saccardo) Petch have also been reported from *Monochamus* species in Japan and may have some potential biological control agents [84].

Similarly, information on the natural enemies of *Monochamus* beetles in Europe is limited. Until 2004, no specific parasitoid of *Monochamus galloprovincialis* Olivier was reported, although generalist braconids such as *Atanycolus genalis* (Thomson) and *Meteorus corax* Marshall are known to parasitize *M. galloprovincialis* [85]. According to Naves et al. [86], no egg parasitoids were found, and larvae parasitism by three Braconidae such as *Cyanopterus flavator* Fabricius, *Iphiaulax impostor* (Scopoli) and *Coeloides sordidator* Ratzeburg was less than 10%.

Burning and chipping pine trees infected by PWD was the main control method employed in South Korea between 1988 and 2001, together with the aerial application of insecticides in 1989. In 2002, a method for felling and fumigation of infected trees with metam-sodium was developed, and this method has been widely applied [87]. Up to 2015, PWD control was carried out mainly with techniques using chemicals such as felling and fumigation, the trunk injection of nematicides, and the aerial spraying of insecticides [63,87]. Since 2015, the use of chemical applications has been reduced due to the concern over environmental contamination, and the felling and crushing of pine trees infected by PWD has become the main control method. Fumigation was conducted in the area where felling and crushing is not applicable because of limited access to the crushing machine. The trunk injection of nematicides is costly and labor intensive, so it is used only for ornamental or nursery trees [12]. For the biological control of the key vectors, the parasitic wasp *S. harmandi* was selected, but there is yet no report of its successful use.

5. Causes of Changes in Dominance of Insect Pests in Korean Forests

The dominant pine forest pests in Korea over the last 50 years has dramatically changed from the PC via the PNGM to PWD. These changes have possibly been caused by bottom-up effects, reflecting changes in forest vegetation including the dominance of pine trees in forest as well as forest environmental conditions. At the same time, top-down effects by natural enemies might also contribute to the stabilization of outbreaks of the PC and the PNGM. The PC and the PNGM directly damage pine trees by defoliating, whereas PWD causes damage by wilting pine trees through the mutualistic interactions between the invasive nematode and native beetle vectors, suggesting that biological traits of the dominant pests as well as the dominant species of forest pests have changed over the last 50 years. Figure 3 presents a schematic diagram for sequential changes in major pine forest pests in Korea relating to invasion history of species and forest management policy.

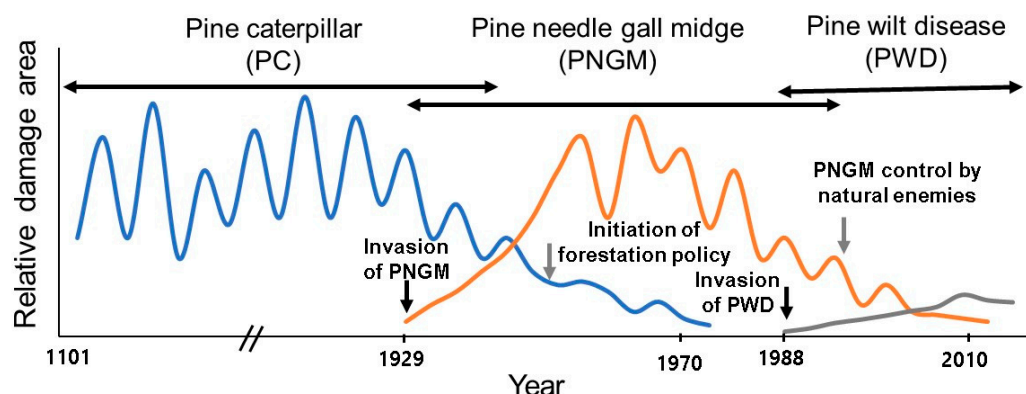


Figure 3. The schematic diagram for sequential changes in major pine forest pests in Korea from pine caterpillar via pine needle gall midge to pine wilt disease. The vertical black arrows indicate the first report of invasive species, and grey arrows indicate the potential causes of decline of pine caterpillar and pine needle gall midge. The first occurrence of pine caterpillar in Korea was reported in 1101 (Goryeo Dynasty) (<http://www.history.go.kr>).

The causes of PC decline could be explained by (1) the longer periodicity in the outbreak of the PC; (2) an increase in activity of natural enemies, including fungal pathogens probably due to reforestation; or (3) inferior competitiveness with the PNGM. Longer periodicity has possibly contributed to recent decline of the PC in Korea. The second hypothesis is related to bottom-up regulation in a forest ecosystem. From the 1950s to the early 1970s, the dominance of the Japanese red pine was at its peak, and the forests consisted of young trees because Korean forests were severely damaged during the Japanese colonial era (1910–1945) and the Korean War (1950–1953) and then intensively used for fuel. These deforested conditions might have promoted PC outbreaks because the PC prefers younger pine trees, and the activities of fungal pathogen were minimized due to lower humidity in the young forests [88]. The last hypothesis is related to the introduction of the PNGM. The main host plants of both the PC and the PNGM are the Japanese red pine and the Japanese black pine. The period of PC decline coincided with the range expansion of the PNGM. Furthermore, host switching of the PC from the Japanese red pine to the pitch pine was observed in late 1990s and early 2000s [24], suggesting that as the inferior competitor to the PNGM (Kwon T.S, unpublished data), the PC fed on the less preferred pitch pine instead of the Japanese red pine [29].

Meanwhile, the decrease in PNGM occurrence could be explained by (1) an increase in tolerance of pine trees to the PNGM; (2) an increase in activities of natural enemies including exotic parasitoids; or (3) the lower performance of the PNGM under higher temperature, thus showing the influence of climate changes. The outbreak of the PNGM was the highest at seven years after the first local invasions. After the first initial outbreak of the PNGM, the mortality of pine trees decreased and stabilized at a low level. Probably, those pine trees most susceptible to the PNGM died in the first invasion and tolerant

individuals survived, or trees that survived the first invasion later acquired resistance to the PNGM. However, there is no evidence to support this hypothesis. The second hypothesis (increase in natural enemies) was tested by several studies [51,53]. Among the four parasitoids of the PNGM, only *I. seoulis* dispersed in similar speed with the PNGM and other parasitoids followed slowly the spread of the PNGM. The interspecific competition between these parasitoids with different phenologies was weak, meaning that more than two parasitoids could act to suppress PNGM populations without strong interspecific competition. Over the long-term, the population of the PNGM decreased with increasing parasitism rates by two or three PNGM parasitoids [51,53]. The last factor is related to the thermal biology of the PNGM, because long-term data analysis suggests that the PNGM is a cool-adapted species [51]. Considering that its adults emerge from late May to early July, an increase in the highest temperature over 30 °C in June due to climate change may have negative impacts on the performance of the PNGM.

6. Perspectives

The occurrence of PWD is still in the expansion phase and the risk of its damage is likely to increase with climate change in South Korea. Meanwhile, there remains very little effect on PWD by natural enemies. Therefore, PWD expansion is likely to increase on the next decades with climate change in South Korea. Considering that outbreaks of the PC and the PNGM decreased due to environmental changes and the activities of natural enemies, however, the outbreak of PWD may decrease due to a reduction in the number of susceptible pine trees or an increase in effective natural enemies of insect vectors. It is likely that mixed species forests can reduce PWD spread. Changes in the major forest pests in pine forests of South Korea over the last 50 years have shown that bottom-up effects, including forest status and biological traits of pest species, likely determined which pest species were dominant, while top-down regulation stabilized outbreaks of the major forest pests. The impacts of the forest pests have increased in terms of tree mortality in the last 50 years. The invasive species have been major threats to forest health, and the influence of climate changes on the performance of forest pests has also been observed. These facts suggest that the decline of pine trees could be accelerated due to forest pests. Therefore, novel management strategies of forest pests in pine trees are needed to sustainably manage pine forests in Korea.

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