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Review

Oak Decline Syndrome in Korean Forests: History, Biology, and Prospects for Korean Oak Wilt

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Abstract: Oak decline syndrome has been observed in South Korea and Japan and variously referred to as Korean oak wilt (KOW) and Japanese oak wilt (JOW). We reviewed aspects of the historical occurrence of KOW, disease cycle, and its potential causes. KOW has been seen principally in Mongolian oak (*Quercus mongolica* Fisch. ex Ledeb.). The first occurrence of KOW was in 2004 in Seongnam, South Korea. KOW is associated with the fungus *Raffaelea quercus-mongolicae*, which is vectored by the ambrosia beetle *Platypus koryoensis*. In addition, it has been suggested that yeasts have evolved a symbiotic relationship with the vector without antagonism for the pathogenic fungus. The number of trees in Korea killed by KOW increased to about 331,000 in 2011, but then decreased to about 157,000 in 2019. We hypothesized that trees infected by *R. quercus-mongolicae* accumulate phenolic compounds in the sapwood and the vector (*P. koryoensis*) beetles then avoid these trees. Therefore, the number of hosts available for the beetle after a KOW outbreak decrease due to accumulation of phenolic compounds in the wood, although most oak trees survive outbreaks. Therefore, *P. koryoensis* beetles move longer distances after outbreaks to find susceptible host trees. Novel occurrence of KOW in Korea may be due to either (1) an increase in tree age (size) in Korean oak stands, for which the beetle has a known preference or (2) climate change, which may be increasing the number of weakened or stressed trees, for which *P. koryoensis* also shows a preference.

Keywords: ambrosia beetle; climate change; long distance dispersal; mutualistic interaction; *Platypus*; *Raffaelea*

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Citation: Choi, W.I.; Lee, D.-H.; Jung, J.B.; Park, Y.-S. Oak Decline Syndrome in Korean Forests: History, Biology, and Prospects for Korean Oak Wilt. *Forests* **2022**, *13*, 964. https://doi.org/10.3390/f13060964

Academic Editor: Zoltán Elek

Received: 9 May 2022
Accepted: 16 June 2022
Published: 20 June 2022

1. Introduction

Oak decline is global phenomenon and one of the severe concerns in forest ecosystem health [1,2]. Among 450 species in *Quercus* genus in the world [3], oak declines were reported for several species such as *Quercus rubra* L., *Quercus velutina* Lam., *Quercus coccinea* Muenchh. And *Quercus alba* L. in USA; *Q. rubra* and *Quercus petraea* (Matt.) Liebl. In Great Britain; *Quercus ilex* L. and *Quercus suber* L. in Spain [1]. Oak decline is related to stresses from various abiotic and biotic factors, alone or in combination [4] that facilitate attack by secondary pests and micro-organisms. Abiotic stressors such as drought, frost, excess moisture, and silvicultural practices can induce attack of secondary pests [2]. Drought is considered particularly important, and various agents such as wood-borers and symbiotic micro-organisms have attacked stressed oak trees in Europe and North America [1].

Declines of cork oak (*Q. suber*) and holm oak (*Q. ilex*) in the western Mediterranean region have been related to attacks of plant pathogenic fungi associated with the buprestid beetle *Coraebus florentinus* (Herbst) [5]. The decline of the oaks is also especially affected by *Phytophthora cinnamomi* Rands [6]. In Iran, acute oak decline of *Quercus castaneifolia* C.A. Mey was associated with presence of the bacteria *Brenneria* spp. and *Rahnella victoriana*

Brady et al. [7]. Among the biotic factors damaging forests, insect pests and diseases are expected to increase as they invade new areas or move to adapt to climate change [1].

The risk of outbreaks of ambrosia beetles and bark beetles is expected to increase as trees are weakened or stressed by climate change [8]. In the case of ambrosia beetles, their mutualistic interaction with fungi and their eusocial brood care increases their ecological fitness under the influence of environmental change [9,10]. In fact, outbreak and biological invasions of ambrosia beetles and their damage to forests are extensively reported [8,10,11]. Korea and Japan have both experienced similar oak decline problems: Korean oak wilt (KOW) [11] and Japanese oak wilt (JOW) [12]. Both diseases occurred in oak species, mainly *Q. mongolica* and *Quercus crispula* Blume for KOW and JOW, respectively [11,12]. However, the fungus and its insect vector are different for KOW and JOW. KOW was induced by *Raffaelea quercus-mongolicae* K.H. Kim, Y.J. Choi and H.D. Shin, sp. nov. vectored by *Platypus koryoensis* (Murayama), whereas JOW was caused by *Raffaelea quercivorus* Kubono et Shin. Ito vectored by *Platypus quercivorus* (Murayama) [13,14].

During the past five decades, the main forest pests in Korea have been species attacking conifers because of such trees' high dominance in Korea [15]. After the successful afforestation efforts made in the 1970s, the dominancy of coniferous species in Korea decreased, while that of oaks increased [15]. With increased oak dominance, the risk of oak tree mortality due to forest insect pests and diseases logically also increased [16]. Therefore, there is a need to better understand the current status of KOW and determine how to manage oak decline effectively.

Here, we reviewed aspects of the historical occurrence of KOW, disease cycle, and its potential causes. Based on the literature, we considered three possible explanations for oak decline in Korea: (1) the roles of pathogen in tree mortality, (2) an increase in size of oaks, and (3) climate change [11]. Finally, the future of KOW was discussed.

2. History of Korean Oak Wilt (KOW)

The first known occurrence of KOW was observed at Ibaejae in Seongnam, South Korea in August, 2004 (Figure 1a), infecting mainly dead Mongolian oak (*Q. mongolica*) and a few *Q. aliena* Blume and *Q. serrata* L., showing exit holes of wood-boring insects [13]. The main wood borer associated with KOW is the ambrosia beetle *P. koryoensis* [17]. Simultaneously, a fungus collected from the dead or infected trees and its associated ambrosia beetle were identified as a new fungal species, *R. quercus-mongolicae* [13]. Based on 18s rDNA and morphological analysis, this species is phylogenetically closest to *R. quercivora*, the causal agent of JOW, than to other *Raffaelea* species [13].

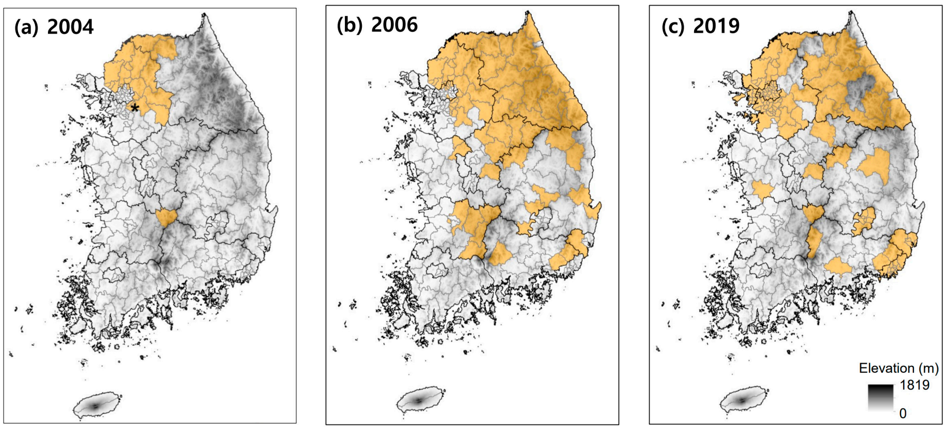

Figure 1. The occurrence areas (yellow color) of KOW in 2004 (**a**), 2006 (**b**) and 2019 (**c**) in South Korea. The asterisk indicates the first occurrence area (i.e., Ibaejae in Seongnam, South Korea) of KOW reported in 2004. The gray color indicates elevation. The graphs were drawn based on data from Annual Report of Monitoring for Forest Insect Pests and Diseases in Korea [18].

In a nationwide survey in 2004, KOW was detected in 18 cities or counties, mainly in the vicinity of Seongnam (Figure 1a). By 2006, KOW had been recorded in 61 cities or counties in the middle of the Korean peninsula (Figure 1a), and the occurrence area expanded slightly in 2019 compared to in 2006 (Figure 1c). The vector beetle of KOW was firstly reported in Korea in 1930 [19], and distribute throughout the country including Jeju island [20]. Therefore, the vector beetle of KOW is considered a native species in Korea. The occurrence pattern showing high occurrence in the northern part of South Korea and the limited occurrence in the southern part would be related with climate variables such as mean daily temperature difference and annual precipitation, elevation and distribution of host plants [21]. The occurrence area of KOW was 1944 ha in 2006 and 4087 ha in 2008. After several fluctuations through to 2013, the area declined to 1576 ha by 2019 (Figure 2a) (http://www.forest.go.kr (accessed on 1 March 2022)). A similar pattern occurred in numbers of trees killed by KOW (Figure 2b).

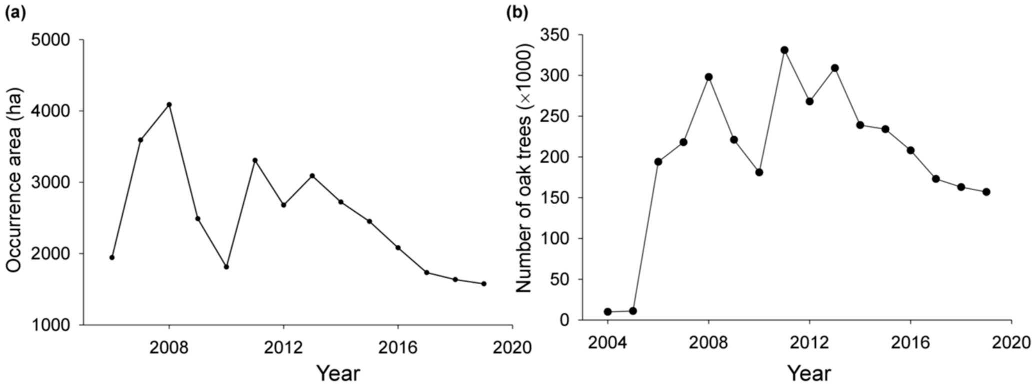

Figure 2. Annual changes in area (ha) damaged (**a**) and the number of dead oak trees (**b**) caused by KOW from 2004 to 2019. The graphs were drawn based on data from Korean Forest Service (www.forest.go.kr (accessed on 1 March 2022)).

Until 2014, the areas with the highest levels of KOW were in and around Seoul [22], although *P. koryoensis* is distributed throughout South Korea, including Jeju island [20]. Monitoring in the vicinity of Seoul from 2011 to 2014 showed that the main KOW areas shifted southward [23]. In 2011, an outbreak of KOW occurred in the Bukhan Mountain National Park in Seoul, and in 2012, 1,585,937 trees spread over 7943.4 ha were infected [24]. In this area, 58.5% of all oak trees were affected by KOW and the mortality of trees infected by KOW was 4.1%. After the mass outbreak of KOW in Bukhan Mountain National Park, the number of infected trees there decreased until 2014 and outbreak of KOW was not observed until 2020 [22].

The distribution of KOW at the regional level was analyzed using satellite images from 2009 to 2014 [22]. Damaged areas were classified based on the density of dead oak trees for the three mountains in Seoul or its vicinity (Bukhan, Cheonggye and Suri mountains). This mapping showed that the highest concentration of KOW was located in the broadleaf or mixed-stand forests with elevations of 200~400 m and slopes of 20~40 degrees, and that a spatial shift of the area with the highest KOW levels occurred from Cheonggye mountain to Suri mountain located 12.5 km to the southwest.

3. Disease Cycle of KOW

3.1. Host and Symptom

The typical symptom of KOW is systematic wilting of oak trees, which occurs when the number of entry holes by *P. koryoensis* is high (Figure 3) [11]. Attack density by the ambrosia beetle vector is the principal factor determining the level of oak mortality caused by KOW [11]. The beetle preferentially attacks the lower trunk, usually on the downslope side because the higher moisture content and thicker phloem on this face are beneficial to the survival of the vector's progeny in the lower trunk, even though more energy is required to penetrate thicker bark in this area [25]. The reason for this is thought to be the less dense tissue in that portion of the tree [11]. When the density of beetles increases, attack also occurs on the higher trunk, possibly to avoid intense intra-specific competition. The presence of *P. koryoensis* entrance holes above 1.5 m indicates high beetle density [11,25]. The spatial distribution of entrance holes was changed from random or contagious to random to reduce intra-specific competition [25].

Figure 3. Mongolian oak (*Q. mongolica*) attacked by *P. koryoensis* (**left**) and wilted by KOW (**right**) (Photos from Park, J.H.).

After attack by *P. koryoensis*, oak trees are also invaded by *R. quercus-mongolicae*, which affects the water-conducting tissues [13]. However, there are no studies on the mechanism by which the fungus causes wilting. In the case of *R. quercivorus*, the causal agent of JOW, cavitation, discoloration, desiccation, and dysfunction of xylem vessels leads to blockage of the upward movement of water after invasion by the fungus. Extensive development of these symptoms in the vessels is considered the cause of severe wilting of the foliage and the subsequent tree death [26]. The presence of extensive discoloration in the wood of trees affected by KOW suggests that trees heavily affected by KOW are killed by a similar mechanism to that of JOW.

The disease cycle of KOW is closely related to the life cycle of *P. koryoensis.* Male beetles make entry holes in oak trees in May and beetle frass is found in the trunk and soil around the trunk [20]. Heavily attacked oak trees die due to systematic wilting in late July to early September (Figure 4). The leaves of dead trees remain on the tree after autumn because oak trees die without the formation of an abscission layer [20] (Figure 3).

Although several different oak species (*Q. mongolica*, *Q. serrata*, *Q. aliena*, *Q. acutissima* Carruth. and *Carpinus laxiflora* (Siebold and Zucc.) Blume) are known to be hosts of KOW in South Korea, *Q. mongolica* is one of the main hosts and is a widely distributed species in South Korea [13]. Suitable habitat for *Q. mongolica* is mainly in the middle of the Korean peninsula, or at areas above 500 m elevation in the southern of Korea [27]. Due to climate change, it was predicted that the area of suitable habitat for this oak would decrease in South Korea in the future [27]. Interestingly, the density of the beetle's entrance holes increased with high dominance of the *Quercus* species [16], suggesting that the probability of KOW increases with available resources of the beetle vector. Similarly, the occurrence of JOW was concentrated in stands with high volumes of *Q. crispula*, a major host of JOW [28].

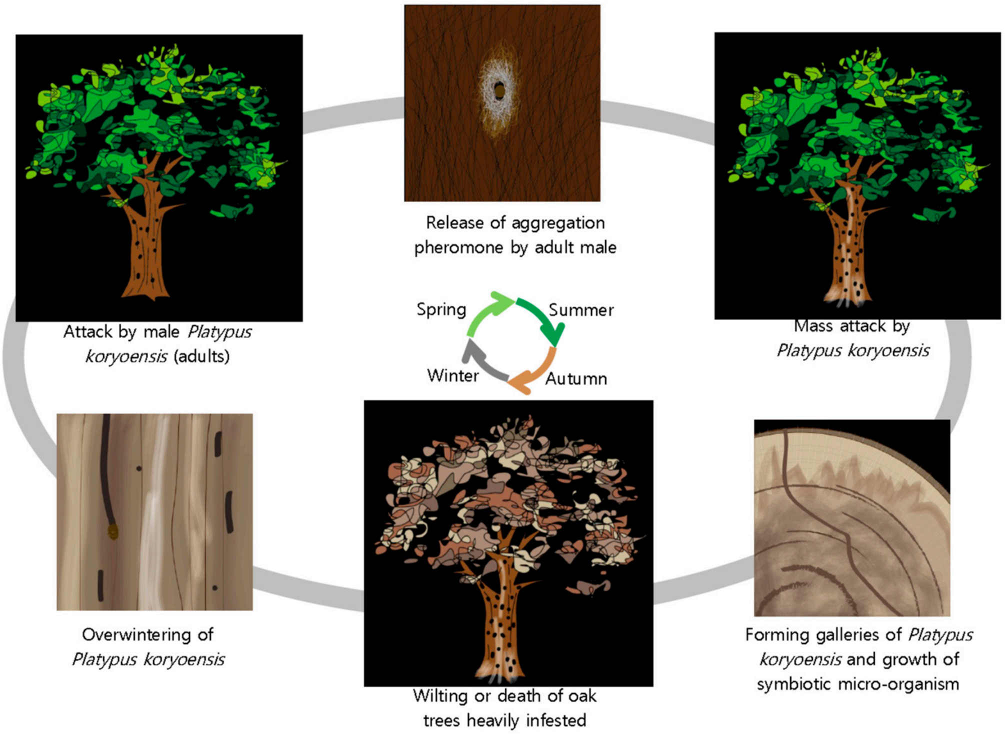

Figure 4. Life cycle of KOW in Korea. The graph was redrawn based on data from research on disease cycle and management of KOW [20].

3.2. Vector Beetle

Ambrosia beetles such as *P. koryoensis* (Platypodinae, Curculionidae) form obligate mutualisms with ophiostomatoid fungi [29]. Platypodinae is a major beetle group showing the fungus gardening behavior [29]. These fungus gardening beetles require a gallery-cleaning behavior by their parents or sisters to avoid contamination of galleries from unwanted fungi [30]. This behavior represents some degree of sociality, and this social behavior is favorable for adaptation to new environments [10]. New outbreaks or invasions to new areas by ambrosia beetles have likely increased due to their social behaviors [8,9].

Among the ambrosia beetles, periodic population outbreaks of the subgroup Platypodinae have been frequently reported throughout the world, and concerns for their economic and ecological impacts have increased [11]. Examples of tree-killing platypodines include *P. quercivorus* on *Quercus* spp. in Japan [31,32], *P. koryoensis* on *Quercus* in Korea [13,33], *Platypus cylindrus* Fabricius on *Castanea* spp., *Fagus* spp. and *Quercus* spp. in Europe [34–36], *Platypus oxyurus* Dufour on *Abies* spp. in Europe [37], and *Megaplatypus mutatis* Chapuis on *Populus* spp. in South America and Europe [38].

The basic biology of *P. koryoensis* was little studied until 2004 when KOW was first reported in South Korea. The beetle was initially identified as *Crossotarsus koryoensis* by Murayama in 1930 [19], and it was collected in 1987 [39]. Its biology was reported by Lee and Chung [40] but there was no report about tree damage until 2004 [33]. Its geographical distribution includes Korea, Taiwan, Japan, and the Russian Far East, although its distribution in Japan is not well known [33]. The presence of *P. koryoensis* in Kyushu, Japan was confirmed through specimen examination (personal communication with Dr. Goto).

P. koryoensis beetles mostly attack larger trees [11], seldom infesting trees less than 20 cm in DBH [25]. The galleries of *P. koryoensis* are horizontal to the ground and mainly in sapwood [11]. It is likely that differences in the chemical composition of sapwood and heartwood explain the beetle's avoidance of heartwood. In case of *Quercus faginea* Lam., phenolic levels were higher in heartwood than sapwood, although lignin and sugar composition were similar [41]. Interestingly, levels of the lignan (−)-lyoniresinol and various phenolic compounds [42] increased in the sapwood of *Q. crispula* in response to attack by *R. quercivora*. This increase in phenolic compounds led *P. koryoensis* to avoid infested wood for new ovipositions, presumably because the beetle interpreted infested sapwood as heartwood [42].

The spatial distribution of the beetle within oak stands, based on attack density in the lower trunks, showed a density-dependent pattern [43]. In low-density beetle populations, attack was concentrated on a few trees for mass attack to overcome host defense. As attack density in stands increases, attacks also occur on non-mass attacked trees. In stand with relatively high beetle density, beetles massively attack new hosts rather than already attacked hosts. Due to this pattern of attacks, the number of damaged trees increases rapidly when beetles are more abundant.

Most species of platypodid beetles exhibit male-initiated monogamy [44], in which male-produced pheromones attract con-specific females. In addition, aggregation pheromones are produced by males of *P. koryoensis*, which have been identified as a mixture of citronellol, nerol, neral, geraniol, and geranial [13]. Although ethanol can attract *P. koryoensis* (as well as other ambrosia beetles, such as *Xyleborus crassiusculus* (Motschulsky), *Xyleborus mutilates* (Blandford) and *Ambrosiodmus lewisi* (Blandford)), the highest catch of *P. koryoensis* was in traps baited with citral or a mixture of neral and geranial, not ethanol, under field conditions [45]. Similarly, quercivorol, (1S,4R)-*p*-Menth-2-en-1-ol, was identified as the aggregation pheromone of *P. quercivorus* [46].

Trap catches of *P. koryoensis* in four oak forests suggested that *P. koryoensis* is univoltine in central Korea [47]. Destructive sampling at monthly intervals of trees infested by *P. koryoensis* provided data on the phenology and age structure of the beetle's life stages [48]. Eggs, larvae, and adults were found throughout the year. However, pupae were abundant only in April and May, although a few were present in July and August, suggesting the beetle is univoltine. Most likely, pupae detected in July and August had developed from eggs laid by adults moving into the forest study site in June. Similarly, the first eggs laid by the ambrosia beetle *Xyleborinus saxeseni* (Ratzeburg) developed into females that either remained in galleries or dispersed late in the season. These females cooperated in care of other brood by tending the fungus gardens, extending the gallery, and feeding and cleaning offspring. The presence of pupae in July and August is also indirect evidence for sister care in *P. koryoensis* and some degree of eusociality.

Using a phenology model based on degree days and field observations, Nam et al. [47] determined that the lower threshold temperature for the development of the beetle is 5.8 °C. The model predicted the median flight date of the beetle within five days [47]. Historical data suggested that the date of the median flight day advanced nine days from 1970 to 2010, probably due to climate change [47].

The beetle's flight distance was estimated using mark–release–recapture methods, marking beetles with fluorescent powders and recovering marked beetles with sticky traps deployed in the oak forest studied [49]. At least 300 individuals were released in each trial at 11:00 a.m. in late June 2013 when beetle flight propensity was greatest, and recaptured individuals were counted after three hours. No marked beetle was recaptured the next day [50]. Recapture efficiency was 6.0 ± 1.6% and the mean dispersal distance was 18.0 ± 1.3 m. The annual movement distance in infested stands in Jinan, Jeollabuk-do was 24.1 m and 19.9 m from 2012 to 2013 and from 2013 to 2014, respectively, showing that the beetle's limited dispersal distance reasonably explained the slow movement of infested stands. A mechanism of long-distance dispersal was proposed to explain movement of beetles over several kilometers. The proposed mechanism postulates that when the beetle density in a tree becomes high, the beetle forms entrance holes in the upper trunk rather than the lower trunk as usual, to reduce intensive intra-specific competition [25]. The beetles emerging from galleries in the upper trunk probably have the potential to fly longer distances, possibly aided by wind (Figure 5). Satellite image analysis showed that KOW hot spots had jumped about 12.5 km per year [22].

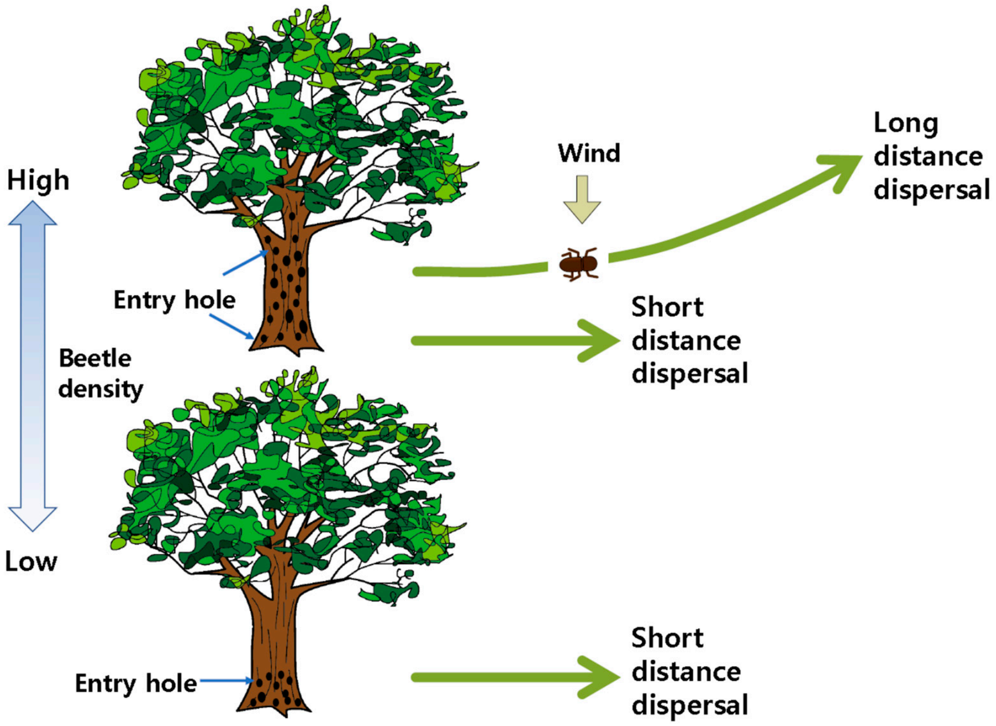

Figure 5. A diagram for hypothesis to explain long distance dispersal of *P. koryoensis* in density-dependent manner. The diagram was drawn based on a hypothesis suggested by Lee et al. [49].

Dispersal pattern of JOW was similar to that of KOW. For *P. quercivorus*, at least half of all trapped adults were found in traps installed <2 m above ground, and trap catch decreased with increasing trap height [51], showing that most beetles flew at less than 2 m height. Local dispersal distances of JOW were also relatively short and less than 100 m but its long-distance dispersal was over 10 km [14]. Flight mill experiments suggested that the flight capacity of *P. quercivorus* is at least 27 km [52], showing the beetle's capacity for long distance dispersal.

3.3. Fungus as the Causal Agent of KOW

Ophiostomatoid fungi have mutualistic interactions with bark or ambrosia beetles, and they have been recognized as potential causal agents for tree mortality in many countries [53–55]. Among these fungi, *Raffaelea* species potentially contributed several observed mass tree mortality events [56–59]. Laurel wilt disease due to *R. lauricola* has caused widespread mortality of several tree species in the family Lauraceae, including avocado in the southeastern United States [60,61]. The impacts of several *Raffaelea* species were considered black swan events (an unpredictable event that is beyond what is normally expected) in tree pathology given that pathogenicity of *Raffaelea* species was either shown to be weak or not proven by artificial inoculation experiments [62].

To test the pathogenicity of *R. quercus-mongolicae*, inoculation trials were performed on both saplings and twigs of mature trees of *Q. mongolica* [63]. The fungus had an ability to colonize sapwood, to contribute to sapwood discoloration and disrupt sap flows, but the pathogenicity of the fungus was not confirmed. The fungus also induced discoloration in the wood of chestnut oak (*Q. acutissima*) when inoculated by artificial injection using Chemjet tree injector, an injector with a steady low pressure [64]. When Japanese oak was artificially inoculated with the fungus, *R. quercivora*, the oak died rapidly with increase in gallery density, which resulted in many offspring. Furthermore, trees with high density of galleries have more discolored areas in wood, and the fungus was frequently re-isolated from the inoculated trees. These recoveries clearly showed that the mass mortality of Japanese oak was caused by mass attack of *P. quercivorus* and its associated fungus, *R. quercivora* [65]. Studies on the spatial distribution of *R. quercivora* in the xylem showed that the hyphae of the fungi were located in the nearby inoculation site and failure of the xylem vessels was associated with the hyphae distribution, suggesting that the oak mortality was caused by massive failure of the xylem vessels due to mass attack by the beetle and its associated fungus [66].

To understand the origin of *R. quercus-mongolicae* in South Korea, the population diversity of 54 isolates of the fungus, collected nationwide (except Jeju island), was determined using the restriction-site-associated DNA (RAD) marker [67]. Based on the lower genetic diversity and no apparent population structure of *R. quercus-mongolicae*, it was suggested that the fungus was introduced to the country, which led to the sudden emergence of KOW on native oaks. However, this view of *R. quercus-mongolicae* as an invasive fungal pathogen is based only on a lower level of genetic diversity and is not in line with other studies. In particular, Lee et al. [68] determined the genetic diversity of 81 isolates of *R. quercus-mongoicae* that were collected from inland areas covering 36 geographical locations in Korea, using microsatellite markers, and found higher levels of genetic indices, supported by other studies [69,70]. In addition to the genetic indices determined by Lee et al. [68], two different mating types of *R. quercus-mongolicae* occurred in equal proportions in the country [71]. Furthermore, the fungus has been isolated from a wide range of native hosts, including *C. laxiflora*, *Castanea* crenata Siebold and Zucc., *Q. acutissima*, *Q. aliena* and *Q. variabilis* Blume without no visible symptoms on the hosts being developed [68], leading to the conclusion that the fungus is a native fungal species rather than an exotic species.

3.4. Yeast

Bark beetles, including the ambrosia beetles, have evolved symbiotic relationships with microorganisms, especially the ophiostomatoid fungi. In addition to the ophiostomatoids, other microbes have symbiotic associations with ambrosia beetles that are potentially related to tree mortality. Yun et al. [72] examined the symbiotic relationships of various yeast species with *P. koryoensis* that were associated with KOW. Eight yeast species belonging to five genera were recovered from *P. koryoensis*. More yeast isolates were recovered from female beetles than males or larvae. Female *P. koryoensis* beetles have mycangia on their body surface where fungal associates are retained. The yeasts isolated from *P. koryoensis* had no antagonistic effects on *R. quercus-mongolicae* when the two were cocultivated in vitro. In addition, among the yeast species isolated from *P. koryoensis*, each produced different extracellular enzymes, suggesting that polymeric wood components would be more efficiently utilized not by a single yeast species, but by a diverse yeast assemblage. It has been suggested that various microorganisms co-occur in the wood of oak, which all have different functions in the formation and maintenance of the galleries of *P. koryoensis*. Similarly, two yeasts, *Candida* sp. and *Candida kashinagacola* Endoh et al., were identified as symbionts of *P. quercivorus* in Japan [73]. These yeasts were abundant in the interior of the gallery of *P. quercivorus*. Volatiles from yeast fermentation such as ethanol attracted beetles because the chemicals can be signal for presence food sources such sugar [74].

4. Management of KOW

The management of KOW has focused primarily on control of the beetle vector. The first control method is to cut heavily infested trees or ones killed by the beetle. The trunks of these trees are then cut into 1 m long bolts and fumigated with metham sodium or dimethylsulfate. As the entrance holes of the beetle are concentrated in lower trunk, the stumps are also fumigated. If the fumigation is not possible, the trunk is cut into 1 m bolts, and these are then split into half and left in the forest without any chemical treatments. During winter, the beetles inside split bolts are generally failed to form galleries, probably due to bolt dehydration. Some of the oak trees in stands heavily damaged by KOW are cut and used as charcoal, wood chips, or sawdust [75,76].

The second control method is to reduce the density of beetles with trapping methods. Mass-trapping of the vector using tree baits is one option. Tree baits are installed in infested stands in late April. Alternatively, to prevent further infestations by beetles from heavily infested beetles or to reduce density of beetle, a two-part mass-trapping method is used. First, sticky vinyl is used to cover the lower trunk up to 2 m from ground to catch emerging beetles and prevent infestation of nearby trees. This method also catches various non-target organisms such as collembola, insects and even small birds [76]. The second method is to replace the sticky vinyl with non-sticky vinyl sheets that lead to a collecting plastic bottle. The probability of catching non-target organisms was reduced [76].

The third control method is to spray the insecticide fenitrothion on the surface of the trunks of all oak trees in an infested stand. Three applications are applied at 10-day intervals in June. This method prevents the infestation of healthy trees. Injection of fungicides were also tested to directly suppress the fungus *R. quercus-mongolicae* [77]. This method has not yet been put to practical use.

5. Causes of KOW

Three hypotheses explaining the sudden outbreak of *P. koryoensis* in Korea have been proposed [11]. The first hypothesis is that *R. quercus-mongolicae* is a new invasive species recently reaching South Korea and novel association between fungus and oak is a potential cause of tree mortality. This hypothesis is partially supported by the low genetic diversity of *R. quercus-mongolicae* based on molecular techniques [67]. However, the existence of two different mating types of *R. quercus-mongolicae* and its higher genetic diversity estimated by microsatellite markers showed that genetic diversity of the fungus was higher than originally thought, and consequently, the fungus is now considered a native rather than an exotic species [68].

The second hypothesis is that warmer temperatures due to climate change have favored *P. koryoensis* over the cold-adapted Mongolian oak. The distribution of this oak ranges from Korea, China, and Siberia to Mongolia, and South Korea is on the southern edge of its distribution. Indeed, KOW is the most concentrated in toward the southern limit of *Q. mongolica*. Although the beetle can attack and successfully colonize other *Quercus* species [33], the beetles preferentially attack *Q. mongolica.* This host preference can be attributed at least partially to climate change because ambrosia beetles prefer to attack weakened or stressed trees [8]. This explanation is consistent with the pattern of JOW in Japan, for which tree mortality is high at lower elevations and extremely low at higher, colder sites (>1000 m) [28].

The last one is related to the age of the Mongolian oaks throughout Korea, given that *P. koryoensis* preferentially attacks larger oak trees and mortality from KOW was higher in large oak trees than in small ones [11,25]. The dominant age class of Mongolian oaks in Korean forests ranged from 30 to 50 years old in 2015 [78]. This tree age structure was attributed to the history of the country's afforestation policy and the restriction on cutting trees in the 1970s [15]. The outbreak of native red oak borer (*Enaphalodes rufulus* Haldeman) on oak species in Arkansas, United State of America in the 1990s and 2000s was observed in stand with over 50-year-old oak trees, suggesting that the increase in tree age is one of important causes for the outbreak [79,80].

Similarly, increase in JOW in Japan was attributed to climate change [81] or abandonment of the management of oak forests [82]. According to Kamata's hypothesis [81], recent climate changes have induced a northern range expansion of *P. quercivorus*, and a novel association between the beetle and *Q. crispula* was formed. This association induced mass mortality of the oak trees because the trees lacked co-evolutionary adaptations to co-exist with the beetle. In contrast, Kobayashi and Ueda's hypothesis [82] is that oak forests in Japan now contain older, larger trees due to cessation of oak forest management including the cutting of older trees. Older oaks in the forest stimulated the outbreak of *P. quercivorus* because such trees were more vulnerable to attack by ambrosia beetles. Shoda-Kagaya, Saito, Okada, Nozaki, Nunokawa and Tsuda [14] further examined both these hypotheses about the cause of JOW by determining the genetic structure of the vector, *P. quercivorus*, using DNA microsatellites. They found that the genetic structure of the beetle's populations was similar to that of the host *Q. crispula* as reported by Okaura et al. [83]. This finding suggests that the geographical genetic structure of the beetle was shaped by co-evolution with the host species. Therefore, Kobayashi and Ueda's hypothesis [82] was better supported by the molecular analysis of the genetic structure of the beetle populations [14].

6. Discussion

The ambrosia beetle *P. koryoensis* cultivates at least two types of microorganisms and engages in eusocial behaviors of kin care with the parental galleries [10]. To cultivate its fungus, *P. koryoensis* forms its gallery low on the trunk because of high moisture content in that part of the tree [25]. Oak wood is not consumed by the beetle, but rather by the symbiotic fungus, which in turn is consumed by the beetle. After entering the tree in newly formed galleries, adults remain there until their offspring emerge from the galleries the following year. Trees died from previous ambrosia beetle attacks are unfavorable for continued cultivation of the symbiotic fungi because of the dryness of the wood. Therefore, tree mortality is unfavorable to the ambrosia beetle.

In contrast, bark beetles attack trees and develop under the bark, feeding on the cambium as larvae. Bark beetles *Ips*, *Tomicus*, *Dendroctonus*, and *Scolytus* often kill their hosts when their densities are high because the extensive destruction of cambium from larval feeding destroys the xylem vessels [84]. Additionally, for bark beetles, wood is the basic food for larvae, although some bark beetles acquire nutrients from fungi that colonize infested wood [85].

Microorganisms play several different ecological roles in KOW. The first is as a food source for the beetle vector. Yeasts and their metabolites are potential food sources for ambrosia beetles because ethanol, a major metabolite of yeasts, attracts ambrosia beetles. The role of *R. quercus-mongolicae*, a weak pathogen, is to suppress the local defense of oak and provide nutrients for yeast growth by fostering the local destruction oak cells. It is likely that ambrosia beetles benefit mutualisms with weak pathogens because tree mortality is not favorable to the beetle. The roles of microorganisms in KOW need to be further studied to understand their ecological roles and contributions to tree mortality.

7. Conclusions

It is likely that the area in South Korea affected by KOW can be expanded, but that the degree of actual damage can be decreased. Most of the oak trees that survive in forests after an outbreak of KOW were infected by *R. quercus-mongolicae*, which probably makes them unsuitable as hosts for *P. koryoensis*. Therefore, the beetles must expand their distribution to find new suitable host trees, exposing beetles to potential mortality factors. Therefore, the probability of a re-occurrence of KOW in forests that have already been damaged by KOW would be low. The fate of trees infected by *R. quercus-mongolicae* is uncertain. Due to extensive discoloration, water conductivity decreases, but the influence of such decreased water conductivity is not yet clear. Physiological or drought-related mass mortality of oak trees already infected by the fungus was not reported during the last ten years. Further research or monitoring of physiological changes in oak trees damaged by KOW are needed. The recent outbreak of KOW suggests that the risk of outbreaks of new pests in deciduous forests is likely to increase because deciduous trees are increasingly dominating Korean forests.

Author Contributions: Conceptualization, W.I.C. and Y.-S.P.; writing—original draft preparation, W.I.C., D.-H.L., J.B.J. and Y.-S.P.; writing—review and editing, all authors. All authors have read and agreed to the published version of the manuscript.

Funding: This study was supported by the National Institute of Forest Science and the 'R&D Program for Forest Science Technology (FTIS 2017042B10-2223-CA01) provided by Korea Forest Service (Korea Forestry Promotion Institute).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: The authors would like to thank Ye-Eun Kim for her help to draw figures.

Conflicts of Interest: The authors declare no conflict of interest.

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