主 論 文 の 要 約

論文題目 : The effect of disturbance by oak wilt disease on litterfall production, forest dynamics, and seedling dynamics in a warm-temperate secondary forest
（暖温帯二次林のリター生産量、森林動態、および実生動態にナラ枯れが及ぼす影響）

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Secondary forest is one of major forest types in the warm-temperate region and accounts for 23% of the total land area in Japan. Forest dynamics and seedling dynamics in warm-temperate secondary forests are influenced not only by human activities but also by natural disturbances such as Japanese oak-wilt disease. Since the 1990s, oak trees including *Quercus serrata*, *Quercus variabilis*, and *Quercus acutissima*, have been attacked by Japanese oak wilt disease (JOW), which is a fungal disease caused by *Raffaelea quercivora*, in warm-temperate secondary forests in Japan. The impact of the JOW on forest structure has been well studied. Meanwhile, although litterfall production, net primary productivity (NPP), and seedling recruitment are vital processes in a forest ecosystem, limited attention has been paid to these processes in the secondary forests afflicted by JOW. Clarifying the effect of JOW disturbance on warm-temperate secondary forests will aid prediction of vegetative changes after the convergence of JOW and support the planning for effective forest management.

This study was conducted in three permanent plots established in the warm-temperate secondary forests in the Kaisho Forest, Seto City, Aichi Prefecture, central Japan. Since 2008, high mortality among Fagaceae species such as *Q. serrata* and *Q. variabilis* by JOW disturbance has been reported in the Kaisho Forest. According to the mortality of *Q. serrata* and *Q. variabilis*, I classified the study period into three periods (1) peak JOW period (2008–2010), (2) late JOW period (2010–2013), and (3) post-JOW period (2018–2020). The objectives of this study were to clarify the effect of JOW disturbance on litterfall production, forest dynamics, and seedling dynamics to characterize the JOW disturbance; and to discuss the direction of the vegetative change after JOW. First, I determined the effects of JOW on the stand structure and litterfall production (Chapter III). Second, I clarified the effects of JOW on the dynamics of tree communities and aboveground NPP in Chapter IV. Third, in Chapter V, I determined the effects of JOW on the dynamics of seedling communities and examined the impact factors on seedling survival. Finally, in Chapter VI, I compared my key findings for forest dynamics, litterfall production, and aboveground NPP in the Kaisho Forest with those reported in other natural disturbance-afflicted forests. I also compared my key findings for environmental conditions and seedling dynamics with those in other natural disturbance-afflicted forests and then concluded the issues of JOW effects on the warm-temperate secondary forests and perspectives for further studies.

In Chapter III, I investigated litterfall production and forest structure using the 6-years litterfall production data and 12-years forest structure data, respectively and compared them among different phases of JOW outbreak to assess the effect of JOW on litterfall production and forest structure. The mean total basal area (BA) values between 2008 and 2020 were 24.96 m^2 ha^{-1} in Plot 1, 35.34 m^2 ha^{-1} in Plot 2, and 34.43 m^2 ha^{-1} in Plot 3. The BA of deciduous trees declined in all three plots between 2008 and 2013/2015 and the BA of evergreen trees gradually increased over time in all three plots. The results of Chapter III revealed the differences in temporal patterns in BA and stem density between deciduous and evergreen trees. Litterfall production was range from 3.58–5.57, 5.91–7.13, 6.71–10.23 Mg ha^{-1} $year^{-1}$ in Plots 1, 2 and 3, respectively. Total annual litterfall and leaf fall showed little change in peak to post-JOW periods and the changes in BA were unrelated to total litterfall and leaf fall. The observed fluctuation in BA in the Kaisho Forest may not have been large enough to clearly reveal the effect of JOW during these periods. Canopy gaps formed by JOW may enhance the recruitment and growth rates of sub-canopy and understory trees.

In Chapter IV, I calculated the mortality, recruitment, and growth rates of tree communities, and estimated the aboveground biomass (AGB) and aboveground NPP, to examine the effect of JOW on the forest dynamics and aboveground NPP. I found substantial temporal variations in mortality and recruitment rates during 12-year study period. The mortality rate declined in all plots during the study period and the recruitment rate increased from the peak to late JOW periods and then declined, except in Plot 3. After JOW infection, widespread wilting of oak trees after JOW infection led to high mortality in the peak JOW period. And the JOW seemed to be converged 12 years after JOW infection began in the Kaisho forest. As many canopy trees wilted by the JOW, canopy gap formed over the forest enhanced the growth of the sub-canopy trees. However, the favored recruitment and growth of sub-canopy and understory trees in 5 years of JOW disturbance might cause competition among trees and canopy closure, which then decreased recruitment and growth rate. The total increment of AGB (ΔAGB) ranged from 1.39–2.68, 2.56–4.53, and 3.05–4.27 Mg $ha^{-1}year^{-1}$, in Plots 1, 2, and 3, respectively. The mean values for aboveground NPP over study period were 6.82 $\pm$ 0.64 Mg ha^{-1} $year^{-1}$ in Plot 1, 9.99 $\pm$ 1.47 Mg ha^{-1} $year^{-1}$ in Plot 2, and 11.42 $\pm$ 1.37 Mg ha^{-1} $year^{-1}$ in Plot 3. The increment of AGB and aboveground NPP varied little over the peak to post-JOW periods. The effect of dead oak trees might be counteracted by increased recruitment rate and tree growth rates.

In Chapter V, I quantified environmental conditions such as canopy openness and soil moisture and seedling functional traits and monitored seedlings during 2018–2020 to compare the differences in environmental conditions and seedling density among the JOW periods. In addition, I used structural equation model (SEM) to explore the factors affecting the seedling survival. Corresponding data obtained in 2009–2013 were also used for the analyses. During 2009–2013 and 2018–2020, 13,010 current year seedlings including 59 woody species, 44 genera, and 21 families were investigated, and 9810 non-current year seedlings including 68 woody species, 51 genera, and 33 families were monitored. I found that the canopy openness, soil water content, and seedling density all fluctuated temporally in JOW-affected, warm-temperate secondary forests, the Kaisho Forest. The light availability gradually improved, and the values for canopy openness in 2020 were approximately 1.60–1.81 times higher than the initial values in 2009. Soil water availability gradually decreased during the study period and the values for soil water content in 2020 were approximately 40.8–56.5% lower than the initial values in 2010. The recruitment of current-year seedlings improved in late JOW period, after 3–5 years disturbed by JOW, through improved light conditions, whereas the recruitment of non-current year seedlings increased following the improvement of current-year seedling emergence. The results of SEM models indicated that the relative importance of the environmental conditions that impact the seedling functional traits changed over JOW periods. The functional traits of current-year seedlings were likely to be affected by soil nutrients in the late JOW period, whereas the litterfall production impacted the functional traits of current-year seedlings in the post-JOW period. Seedlings with large seed mass, high tree height and root length such as *Q. serrata*, *Q. variabilis*, and *Q. glauca* tended to establish in the area with low CN ratio, S, and high Na in the late JOW period. The relative importance of different factors for seedling survival also varied with changes in the environmental conditions through the JOW periods. The seedling survival was enhanced by increased canopy openness in the late JOW period, and by few litterfall, high soil nutrient content and soil moisture in the post-JOW period. Although the fluctuation in litterfall production in the study site is unlikely to be extreme (Chapter III), the gradual increment of evergreen trees' BA might change not only the quantity of litterfall but also the quality of litterfall, which may influence the seedling survival. The lack of any direct effect of seedling functional traits on seedling survival might be due to the drastic changes in abiotic conditions by JOW disturbance.

The results of this study revealed that the effects of JOW on a warm-temperate secondary forest differ from those of other short-term intense natural disturbances such as hurricanes and typhoons. Although JOW affected the forest structure and forest dynamics, as the damage of JOW was limited compared to that caused by other natural disturbances, litterfall production, ΔAGB, and aboveground NPP appear to be unaffected by JOW during peak to post-JOW periods. As the evergreen trees are increasing after JOW and the quality of the litter generally differs between deciduous and evergreen tree species, further studies for the decomposition of litterfall, nutrient cycling, and belowground NPP are needed for the better understanding of JOW effect on the function of the forest ecosystem. The temporal patterns of the environmental conditions and seedling densities that occurred after the JOW also differed from those observed in the forests impacted by the other natural disturbances (Chapter V). When the amount of litterfall production increases and light conditions decrease according to the forest recovery and succession in the future, the species composition of tree seedlings might vary over time and seedlings of *Q. glauca* are predicted to be likely to establish.

Although forest diseases have been reported to disturb more than 12.5 million hectares of forest in the world and the studies of forest disease effect are still limited. Focusing on the changes in forest structure and function for the whole disturbance period including the initiation of the outbreak is important to determine the effects of disease disturbance on the forest ecosystem. Among statistical tools to describe the factors that influence seedling regeneration, SEM is a powerful tool to estimate both direct and indirect effects. However, as the predictive power of the SEM models is usually low, additional long-term data for seedling dynamics and environmental conditions and functional traits data for more seedling species are needed to enlarge the sample size.