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Changes in understory species occurrence of a secondary broadleaved forest after mass mortality of oak trees under deer foraging pressure

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The epidemic of mass mortality of oak trees has affected secondary deciduous broadleaved forests that have been used as coppices in Japan. The dieback of oak trees formed gaps in the crown that would be expected to enhance the regeneration of shade-intolerant pioneer species. However, foraging by sika deer *Cervus nippon* has also affected forest vegetation, and the compound effects of both on forest regeneration should be considered when they simultaneously occur. A field study was conducted in Kyôtô City, Japan, to investigate how these compound effects affected the vegetation of the understory layer of such a forest. The presence/absence of seedlings and saplings was observed for 200 quadrats sized 5 m × 5 m for each species in 1992, before the mass mortality and deer encroachment, and in 2014 after these effects. A hierarchical Bayesian model was constructed to explain the occurrence, survival, and colonization of each species with their responses to the gaps created or affected by the mass mortality of oak trees. The species that occurred most frequently in 1992, *Eurya japonica*, *Quercus glauca*, and *Cleyera japonica*, also had the highest survival probability. Deer-unpalatable species such as *Symlocos prunifolia* and *Triadica sebifera* had higher colonization rates in the gaps, while the deer-palatable species *Aucuba japonica* had the smallest survival probability. The gaps thus resulted in promoting the colonization of deer-unpalatable plant species such as *Symlocos prunifolia* and *Triadica sebifera*. It might be forecasted that such deer-unpalatable species will dominate the gaps created or affected by the mass mortality of oak trees.
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ABSTRACT

The epidemic of mass mortality of oak trees has affected secondary deciduous broadleaved forests that have been used as coppices in Japan. The dieback of oak trees formed gaps in the crown that would be expected to enhance the regeneration of shade-intolerant pioneer species. However, foraging by sika deer Cervus nippon has also affected forest vegetation, and the compound effects of both on forest regeneration should be considered when they simultaneously occur. A field study was conducted in Kyôto City, Japan, to investigate how these compound effects affected the vegetation of the understory layer of such a forest. The presence/absence of seedlings and saplings was observed for 200 quadrats sized 5 m × 5 m for each species in 1992, before the mass mortality and deer encroachment, and in 2014 after these effects. A hierarchical Bayesian model was constructed to explain the occurrence, survival, and colonization of each species with their responses to the gaps created or affected by the mass mortality of oak trees. The species that occurred most frequently in 1992, Eurya japonica, Quercus glauca, and Cleyera japonica, also had the highest survival probability. Deer-unpalatable species such as Symplocos prunifolia and Triadica sebifera had higher colonization rates in the gaps, while the deer-palatable species Aucuba japonica had the smallest survival probability. The gaps thus resulted in promoting the colonization of deer-unpalatable plant species such as Symplocos prunifolia and Triadica sebifera. It might be forecasted that such deer-unpalatable species will dominate the gaps created or affected by the mass mortality of oak trees.

Keywords: deer-unpalatable plant species, gap, Japanese oak wilt, sika deer, understory vegetation

INTRODUCTION

Many coppices have been abandoned for socio-economic reasons, such as the replacement of woody fuels with fossil fuels in Europe (Rackham, 2008; Müllerová et al., 2015; Svaték and Matula, 2015). This abandonment parallels that of Japan (Suzuki, 2013), and a considerable number of deciduous oak forests grown from such coppices have suffered from the mass mortality of oak trees (Kuroda et al., 2012; Nakajima and Ishida, 2014). This mass mortality has been caused by Japanese oak wilt (Kuroda et al., 2012),
a pathogenic species of fungus *Raffaelea quercivora* Kubono et Shin. Ito, which is carried by the ambrosia beetle *Platypus quercivorus* Murayama (Kubono and Ito, 2002; Kinuura and Kobayashi, 2006).

The mass mortality altered the structures of damaged oak forests. The two major deciduous oak species in Japan, *Quercus crispula* Blume and *Quercus serrata* Murray, are vulnerable to the pathogenic fungus. Nakajima and Ishida (2014) showed that 80 ± 19% (mean ± standard deviation) stems of *Quercus crispula* died while 34 ± 19% stems of *Quercus serrata* died. How such damaged oak forests are regenerated depends on circumstance; sub-canopy trees might grow to canopy trees in some cases (Itô et al., 2009), and dense floor vegetation such as dwarf bamboo might inhibit regeneration in other cases (Itô et al., 2011; Saito and Shibata, 2012). In the latter case, the damaged forests may lack a canopy layer for a long time.

For the last several decades, one of the most serious problems for forest vegetation is impact by deer in Europe and North America (Rooney, 2001; Côté et al., 2004; Rackham, 2008). This is also paralleled in Japan: sika deer (*Cervus nippon* Temminck) is the major inhibitor of forest regeneration (Takatsuki, 2009; Iijima and Nagaike, 2015). However, little is known about how regeneration proceeds after mass mortality under deer foraging pressure (Obora et al., 2013). Gap formations should improve light conditions on the forest floor and promote the regeneration of many tree species (Suzuki, 2013). However, deer browsing should inhibit regeneration except for unpalatable species (Shimoda et al., 1994). Therefore, a combination of both factors might promote the regeneration of species that are unpalatable to deer. This in turn may change the species composition of damaged forests in the future.

It is important for the management of secondary forests to predict what tree or shrub species will be recruited in forest stands damaged by the mass mortality of oak trees and deer impact. In a previous study, Itô (2015) described the changes in the canopy/sub-canopy and understory layers of a damaged forest by comparing before and after the occurrence of mass mortality of oak trees and deer foraging. It was found for the understory layer that regenerating species were limited to the originally abundant species, such as *Quercus glauca* Thunb., *Cleyera japonica* Thunb., and *Eurya japonica* Thunb. var. *japonica*, as well as to species unpalatable to deer, such as *Symplocos prunifolia* Siebold et Zucc. and *Triadica sebifera* (L.) Small. However, the study only described the changes in species occurrence and failed to estimate the specific probabilities of survival and colonization. In this study, the previous data were reanalyzed using a statistical model to more precisely estimate those parameters for each species in the understory layer. This should enable us to forecast which species will dominate such stands in the future.

**MATERIALS AND METHODS**

**Study site**

The field data were collected in the Ginkakuzi-san National Forest located in Kyōto City, Japan (35.029°N, 135.801°E). The yearly average temperature from 1981 to 2010 was 15.9°C and the average precipitation in the same term was 1491.3 mm at the Kyōto Local Meteorological Office. Altitude of the forest was about 100-290 m above sea level, and the forest was in the warm temperate zone. The national forest was protected
for its landscape and the prevention of earth outflow, and most of it was situated in
the buffer zone of the UNESCO world heritage, historic monuments of ancient Kyōto.
The Kyōto-Ōsaka District Forest Office and Forestry and the Forest Products Research
Institute agreed to conduct the study cooperatively in the national forest.

In the 1930s, most of the forest was covered with a mix of pines (Pinus densiflora
Siebold et Zucc.) and broadleaved trees including oak (Quercus serrata). After the
1960s, many pine trees had died due to the pine wilt disease. Recently, most of the
national forest has been covered with a secondary broadleaved forest consisting of
many species such as evergreen oak Quercus glauca, evergreen subcanopy species
Symlocos prunifolia, and deciduous tree species Ilex macrophylla Miq., although conifers
(Cryptomeria japonica (L.f.) D.Don and Chamaecyparis obtusa (Siebold et Zucc.)
Endl.) were planted in a small part of the area (Itō, 2007). In the last decade, the mass
mortality of oaks has damaged the forest. In addition, damages by sika deer such as
browsing and bark-stripping have been noticeable over the same period (Itō, 2015).

In 1992, a study plot sized 0.5 ha (100 m × 50 m) was settled on a south-facing slope
in the national forest at an altitude of about 142-194 m. The average slope inclination
was about 30°and the surface geology was granite. All the stems in the plot were marked
and their diameters at breast height (dbh) were measured in 1993, 1996, 1999, 2002,
2005, and 2014. Mainly due to the mass mortality of oak trees Q. serrata, the basal
area in the plot was decreased from 43.3 m²/ha in 2005 to 39.5 m²/ha in 2014, while
the number of stems in the plot increased from 1554 to 1645. There were 36 Quercus
serrata stems in the plot in 2005, and 21 of them died by 2014. Almost all seemed
to be killed by Japanese oak wilt. This affected the forest structure in the plot via the
formation of new canopy gaps or additive disturbance to existing gaps Itō (2015). On
the other hand, none of the evergreen oaks Quercus glauca died from the disease though
some were attacked by the ambrosia beetles, being less vulnerable than Quercus serrata
(Murata et al., 2005, 2009). In the understory layer, Quercus glauca and some evergreen
shrub species such as Eurya japonica and Cleyera japonica were frequently observed.
Overall changes in the stand composition of the site from 1990s to 2010s were reported
in Itō (2015).

Data collection

The plot was divided into 200 quadrats sized 5 m × 5 m. In 1992, all woody plant
seedling or saplings (age ≥ 1 year and dbh < 3 cm) were searched for throughout each
quadrat, and the species names of found seedlings and saplings were recorded. The
same observation was conducted again in 2014. In 2004, each quadrat was classified
into inside or outside of the gaps, which were formed by death of oak trees, or had been
gaps at least since 2005 and were affected in addition by fallen dead oak trees. Twenty
of 200 quadrats were classified as gaps created or affected by oak death. The size of the
largest gap was approximately 250 m² consisting of 10 adjacent quadrats.

In 1992, 55 species were observed and 58 species in 2014 (Itō, 2015). The following
analysis was conducted for 42 of the species that were observed in more than 5 of 400
occasions (200 quadrats × 2 observations).
A hierarchical Bayesian model was constructed to explain which species benefited or were damaged in the understory layer by the recent environmental changes in the forest. The presence/absence (presence = 1, absence = 0) of species $i$ in quadrat $j$ in the year 1992 ($y_{1ij}$) and 2014 ($y_{2ij}$) was assumed to follow the Bernoulli distribution given the occurrence probability $\psi_{1ij}$ and $\psi_{2ij}$, as follows,

$$y_{1ij} \sim \text{Bernoulli}(\psi_{1ij})$$
$$y_{2ij} \sim \text{Bernoulli}(\psi_{2ij}).$$

To be exact, the “presence/absence” was “detection/nondetection” (Dorazio et al., 2006; Kéry and Schaub, 2012). It has been pointed out that detection probability should be considered to correctly estimate population properties such as the occurrence rate or survival rate, even if the observed objects are plants (Kéry, 2004; Chen et al., 2009, 2013). The present study had, regrettably, only one observation for each survey year. However, the quadrat size was rather small (5 m $\times$ 5 m) and the whole of each quadrat was explored, so I expected that the detection probability should be near to one and therefore “detection/nondetection” was regarded as “presence/absence” in this study. Chen et al. (2009) showed that the detection probability asymptotically approaches one with larger survey efforts.

The parameter of occurrence in 1992, $\psi_{1ij}$, was formulated as follows,

$$\text{logit}(\psi_{1ij}) = \beta_o + \varepsilon_{oi} + r_j,$$

where $\beta_o$ denotes an intercept or overall mean of $\psi_1$ on the logit scale, and $\varepsilon_{oi}$ denotes the species random effect on the intercept of species $i$. The parameter $r_j$ denotes a spatially autocorrelated random effect of quadrat $j$.

The parameter of occurrence in 2014, $\psi_{2ij}$, was formulated as follows,

$$\psi_{2ij} = y_{1ij}\phi_{ij} + (1 - y_{1ij})\gamma_{ij},$$

where parameter $\phi_{ij}$ denotes the ‘survival’ probability that species $i$ was present in quadrat $j$ in 1992 and still present in 2014. The parameter $\gamma_{ij}$ denotes the ‘colonization’ probability that species $i$ was absent in quadrat $j$ in 1992 but present in 2014.

The parameters of survival $\phi_{ij}$ and colonization $\gamma_{ij}$ were formulated as follows,

$$\text{logit}(\phi_{ij}) = \beta_s + \varepsilon_{si} + (\beta_{sg} + \varepsilon_{sgi})g_j,$$
$$\text{logit}(\gamma_{ij}) = \beta_c + \varepsilon_{ci} + (\beta_{cg} + \varepsilon_{cgi})g_j,$$

where the parameters $\beta_s$ and $\beta_c$ are intercepts or overall means of $\phi$ and $\gamma$ on the logit scale, respectively. The parameters $\varepsilon_{si}$ and $\varepsilon_{ci}$ are species random effects on the intercepts, $\beta_{sg}$ and $\beta_{cg}$ are coefficients of the gap covariate $g_j$ (0: non-gap quadrats, 1: gap quadrats affected by oak mortality), and $\varepsilon_{sgi}$ and $\varepsilon_{cgi}$ are species random effects on the coefficients.

Priors of the species random effects were defined hierarchically; hyperparameters, $\sigma_o$, $\sigma_s$, $\sigma_{sg}$, $\sigma_c$ and $\sigma_{cg}$, scaled the distribution of $\varepsilon_{oi}$, $\varepsilon_{si}$, $\varepsilon_{sgi}$, $\varepsilon_{ci}$ and $\varepsilon_{cgi}$, respectively, as follows,
where Normal(0, $\sigma^2_o$)T($-10, 10$), denote a normal distribution truncated between -10 and 10; the truncation was incorporated to stabilize the logit scale parameters (Kéry and Schaub, 2012). Priors of the parameters $\beta_o$, $\beta_{op}$, $\beta_{os}$, $\beta_s$, $\beta_{sg}$, $\beta_c$, and $\beta_{cg}$ were defined as Normal($0, 10^4$)T($-10, 10$). The prior of the spatial effect $r_j$ was defined as an intrinsic conditional autoregressive model as follows,

$$r_j \mid r_{-j} \sim \text{Normal} \left( \sum_{k \neq j} w_{jk} r_j, \frac{\sigma_r^2}{w_{j+}} \right),$$

where $r_{-j}$ denote the values of $r$ except the quadrat $j$, a variable $w_{jk}$ was defined to be 1 if quadrat $j$ and quadrat $k$ are adjacent, and 0 if not, and $w_{j+}$ was defined to be $\sum_k w_{jk}$. The parameter $\sigma_r^2$ denotes a variance of the random effect.

Presence/absence data of 42 species, which were observed in more than 5 quadrats in total combining 2 survey occasions, 1992 and 2014, were used for the parameter estimation. The parameters were estimated using the Markov chain Monte Carlo (MCMC) method. Four parallel chains were generated, and each of them had 13,000 iterations while the first 3,000 iterations were dropped as burn-in. The MCMC sample was taken from the three chains with 10 thinning intervals, so that the sample size was 4,000. OpenBUGS 3.2.3 (Lunn et al., 2009) was used for the computation. The BUGS code is available in List S2.

RESULTS

The MCMC calculation seemed to be successfully converged; Gelman-Rubin statistics ($\hat{R}$) were no larger than 1.1 for each parameter (Gelman and Rubin, 1992; Brooks and Gelman, 1998). However, some random species effects on coefficients of gaps had rather wide posteriors such as in Quercus glauca (Fig. 3B). Those parameters might lack enough information to estimate precise posteriors due to the small number of colonizers in the gap quadrats for those species.

Posterior mean, median, and 95% CI (Credible Interval) of the overall occurrence probability in 1992, $\beta_o$, was estimated to be -3.25 for the posterior mean, -3.25 for the median, and -3.99 – -2.54 for the 95% CI, equivalent to 0.037, 0.037, and 0.018 – 0.073 on the probability scale, respectively (Table 1). The overall survival probability, $\beta_s$, was estimated to be -2.60 for the posterior mean, -2.57 for the median, and -4.11 – -1.44 for the 95% CI, equivalent to 0.069, 0.071, and 0.016 – 0.019 on the probability scale, respectively. The overall colonization probability, $\beta_c$, was estimated to be -3.81 for the posterior mean, -3.81 for the median, and -4.45 – -3.18 for the 95% CI, equivalent to 0.022, 0.022, and 0.012 – 0.040 on the probability scale, respectively.

Posterior mean of coefficients of the gap on the survival $\beta_{sg}$ and colonization $\beta_{cg}$ were -0.17 and 1.51, respectively, and $\beta_{cg}$ did not include zero in the 95% CI (0.86 – 2.08), while $\beta_{sg}$ included zero in the 90% CI (-1.27 – 0.81).

Random species effects on occurrence probability in 1992 ($\varepsilon_o$) are shown in Fig. 1. Eurya japonica, and Quercus glauca had the largest value, followed by Aucuba japonica,
Table 1. Parameter estimates other than random effects

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>5%</th>
<th>50%</th>
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<th>97.5%</th>
</tr>
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<tr>
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<td>0.37</td>
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<td>-3.88</td>
<td>-3.25</td>
<td>-2.65</td>
<td>-2.54</td>
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<tr>
<td>$\beta_s$</td>
<td>-2.60</td>
<td>0.67</td>
<td>-4.11</td>
<td>-3.81</td>
<td>-2.57</td>
<td>-1.61</td>
<td>-1.44</td>
</tr>
<tr>
<td>$\beta_{sg}$</td>
<td>-0.17</td>
<td>0.65</td>
<td>-1.54</td>
<td>-1.27</td>
<td>-0.14</td>
<td>0.81</td>
<td>1.04</td>
</tr>
<tr>
<td>$\beta_c$</td>
<td>-3.81</td>
<td>0.32</td>
<td>-4.45</td>
<td>-4.33</td>
<td>-3.81</td>
<td>-3.28</td>
<td>-3.18</td>
</tr>
<tr>
<td>$\beta_{cg}$</td>
<td>1.51</td>
<td>0.31</td>
<td>0.86</td>
<td>0.98</td>
<td>1.53</td>
<td>1.99</td>
<td>2.08</td>
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<tr>
<td>$\sigma_o$</td>
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<td>1.76</td>
<td>1.82</td>
<td>2.24</td>
<td>2.81</td>
<td>2.95</td>
</tr>
<tr>
<td>$\sigma_s$</td>
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<td>0.57</td>
<td>1.97</td>
<td>2.07</td>
<td>2.84</td>
<td>3.91</td>
<td>4.13</td>
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<td>$\sigma_{sg}$</td>
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<td>1.86</td>
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</tr>
<tr>
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<td>0.44</td>
<td>0.60</td>
<td>0.65</td>
</tr>
</tbody>
</table>

SD: Standard Deviation.

Cleyera japonica, Ilex crenata, Photinia glabra, and so on. On the other hand, Carpinus tschonoskii, Celtis sinensis, Zanthoxylum ailanthoides, and Triadica sebifera had the smallest values because these species were not detected in 1992 (Fig. 1). Random species effects on intercept of survival ($\varepsilon_s$) are shown in Fig. 2A. Quercus glauca had the largest value, and Cleyera japonica, Eurya japonica, Camellia japonica L., and Symplocos prunifolia followed. The posterior of Aucuba japonica Thunb. var. japonica was less than zero within 95% CI (Fig. 2A). Random species effects on the survival coefficients of gap covariates were rather small and included zero in their 90% CI for all species (Fig. 2B). Random species effects on intercepts of colonization were the largest in Quercus glauca, followed by Eurya japonica, Cleyera japonica, Symplocos prunifolia, Photinia glabra (Thunb.) Maxim., and so on (Fig. 3A). Random species effects on the colonization coefficient of the gap were the largest in Callicarpa mollis Siebold et Zucc., followed by Zanthoxylum ailanthoides Siebold et Zucc., Carpinus tschonoskii Maxim., Triadica sebifera and so on. They were the smallest in Cleyera japonica (Fig. 3B).

Complete estimates of random effects are available in Table S3.

DISCUSSION

The posterior mean of overall occurrence probability in 1992 was estimated to be -3.25, equivalent to 0.037 on the probability scale; this meant that a species was expected to occur in only 3.7% of quadrats. However, the random species effect on occurrence widely varied; the posterior mean of $\varepsilon_o$ ranged from -3.21 (Carpinus tschonoskii) to 5.71 (Eurya japonica) (Fig. 1). The expected occurrence probability would be 0.00 ($= \logit^{-1}(-3.25 - 3.21)$) for Carpinus tschonoskii and 0.92 ($= \logit^{-1}(-3.25 + 5.71)$) for Eurya japonica. The most frequent species in 1992 were all evergreen tree or shrub species such as Eurya japonica, Quercus glauca, Aucuba japonica, Cleyera japonica, Ilex crenata Thunb., and Photinia glabra. On the other hand, the least occurring species were deciduous trees or shrubs such as Castanopsis tschonoskii, Zanthoxylum ailanthoides, Celtis sinensis Pers., and Triadica sebifera; these species were not detected...
Figure 1. Random species effects on occurrence in 1992 $\varepsilon_0$.
Thin lines denote 95% credible intervals (CI), thick lines denote 90% CI, and circles denote medians.
Figure 2. Random species effects on survival.  
(A) \( \varepsilon_s \), on the intercept, (B) \( \varepsilon_{sp} \) and (B) \( \varepsilon_{sg} \), on the coefficient of the gap. Thin lines denote 95% credible intervals (CI), thick lines denote 90% CI, and circles denote medians.
Figure 3. Random species effects on colonization. (A) $\varepsilon_c$, on the intercept and (B) $\varepsilon_{cg}$, on the coefficient of the gap. Thin lines denote 95% credible intervals (CI), thick lines denote 90% CI, and circles denote medians.
in the quadrats in 1992. The canopy of the forest was almost closed in 1992, so that shade-tolerant evergreen tree or shrub species dominated the understory layer and deciduous early-successional species infrequently occurred.

The posterior mean of survival intercept was largest in *Quercus glauca* (Fig. 2A); the posterior mean was 5.484 and the expected survival probability without the gap effects was estimated to be 0.97 ($= \text{logit}^{-1}(-2.60 + 5.93)$). *Cleyera japonica*, *Eurya japonica*, and *Camellia japonica* followed. These are all evergreen broadleaved species that can survive under a closed canopy, as shown by their occurrence. On the other hand, *Aucuba japonica*, a species of evergreen shrub, had the smallest survival probability; the posterior mean of the random effect was -3.80 and the expected value of survival probability was 0.00 (the calculation was the same as above). *Aucuba japonica* is known to be a food plant for sika deer and is vulnerable to deer browsing (Hashimoto and Fujiki, 2014). The encroachment of deer likely explains its small survival probability. The posterior mean of the random effect was the second smallest in *Vaccinium bracteatum* Thunb. There are relatively small amounts of data on the palatability of *Vaccinium bracteatum* for sika deer, and some reports refer to it as a food plant while others refer to it as unpalatable (Nakajima, 1929; Kabaya, 1988; Takatsuki, 1989; Hashimoto and Fujiki, 2014). The present results suggest that the species is vulnerable to deer impacts.

The random species effects on the coefficients of gap covariates seemed relatively small (Fig 2B). They contained 0 within their 90% CI for all species. This indicates that species heterogeneity in survival may be small within gaps, but that may be due to few light-demanding species occurring in 1992.

The posterior mean of colonization intercept was largest also in *Q. glauca* (Fig. 3A); the posterior mean was 6.09 and the expected survival probability without the gap effects was estimated to be 0.91 ($= \text{logit}^{-1}(-3.81 + 6.09)$).

Random species effects on the colonization coefficient of the gap covariate was the largest in *Callicarpa mollis*, followed by *Zanthoxylum ailanthoides*, *Carpinus tschonoskii*, and *Triadica sebifera* (Fig. 3B). The four species whose colonization probabilities were largest in the gaps are all shade-intolerant (Shimoda et al., 1994; Shibata and Nakashizuka, 1995). In addition, the following *Symplocos prunifolia* is also considered a shade-intolerant species though it is an evergreen species (Fujii, 1994). However, *Symplocos prunifolia* and *Triadica sebifera* are unpalatable plants for sika deer (Shimoda et al., 1994; Hashimoto and Fujiki, 2014). *Triadica sebifera* is an alien species in Japan. The species is unpalatable for sika deer (Shimoda et al., 1994; Hashimoto and Fujiki, 2014), and it is increasing on Mt. Kasugayama (Maesako et al., 2007). Shimoda et al. (1994) studied the deer effects on pioneer species on Mt. Kasugayama in Nara, which is located about 40 km south of the study site and is inhabited by many deer; the authors found that pioneer species including *Zanthoxylum ailanthoides* and *Callicarpa mollis* emerged in gaps but rarely survived or matured due to deer foraging pressure.

*Quercus glauca* originally occurred in most parts of the site, and the survival probability of the species was large, but it also food plant for sika deer (Hashimoto and Fujiki, 2014).

In the study site, small amounts of large plants (height $\geq$ 50 cm) of *Zanthoxylum ailanthoides*, *Callicarpa mollis*, and *Carpinus tschonoskii* were found, though large amounts of those of *Quercus glauca*, *Cleyera japonica*, and *Eurya japonica* were found in the quadrats that were not affected by the mass oak mortality (Itô, 2015). The latter
species are evergreen trees or shrubs, and they had been dominant at least since 1992. In addition to these species, large plants of *Symlocos prunifolia* and *Triadica sebifera* were found in the gap quadrats created or affected by the mass mortality (Itô, 2015), and the large amounts of their saplings and seedlings might contribute to their survival.

**CONCLUSION**

Gaps created or affected by the mass mortality of oak trees might be beneficial for pioneer species. Shade-intolerant species such as *Callicarpa mollis*, *Zanthoxylum ailanthoides*, *Carpinus tschonoskii*, *Triadica sebifera*, and *Symlocos prunifolia* were estimated to more frequently colonize the gaps. In addition, deer-unpalatable species *Symlocos prunifolia* and *Triadica sebifera* may be more likely to survive or mature under foraging pressure of deer, and this may change the species composition in regenerated stands.

In the future, deer-unpalatable species such as *Symlocos prunifolia* and *Triadica sebifera* may dominate the understory rather than the current dominant species such as *Eurya japonica* and *Quercus glauca* within the gaps created or affected by mass mortality of oak trees.

**ACKNOWLEDGEMENTS**

I thank Dr. K. Hirayama (Kyōto Prefectural University) for cooperating with the fieldwork and the Kyōto-Ōsaka District Forest Office for supporting this work. I also thank Dr. H. Iijima (Yamanashi Forest Research Institute) for reading a previous version of the manuscript and for comments. Computational calculations were conducted on the high performance cluster computing system of AFFIT, Ministry of Agriculture, Forestry and Fisheries, Japan.

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