

Changes in the effects of neighboring trees on tree growth and mortality in a temperate mixed forest for 30 years

Enoki, Tsutomu

Division of Forest Environmental Sciences, Department of Agro-environmental Sciences, Faculty of Agriculture, Kyushu University

Hishi, Takuo

Division of Forest Environmental Sciences, Department of Agro-environmental Sciences, Faculty of Agriculture, Kyushu University

Tashiro, Naoaki

Division of Forest Environmental Sciences, Department of Agro-environmental Sciences, Faculty of Agriculture, Kyushu University

<https://doi.org/10.15017/1913927>

出版情報：九州大学農学部演習林報告. 99, pp.1-7, 2018-03. 九州大学農学部附属演習林
バージョン：
権利関係：

Changes in the effects of neighboring trees on tree growth and mortality in a temperate mixed forest for 30 years

Tsutomu Enoki^{*1}, Takuo Hishi¹, Naoaki Tashiro¹

We compared the effects of tree size and the basal area of neighboring trees on the growth rate and mortality of individual trees over the past 30 years (1984-2014), before and after the increase of a sika deer population in a mixed conifer-broadleaf forest in the Shiiba Research Forest of Kyushu University in Japan. In the study site, sika deer (*Cervus nippon*) have reduced understory vegetation since the 1990s, denuding it since the 2000s. Most of the recruitment in the second half of the study period (1996–2014) consisted of tree species that sika deer cannot consume, such as *Illicium anisatum* and *Pieris japonica* subsp. *japonica*. Smaller trees had higher mortality throughout the study period. Neighboring trees affected the tree mortality significantly in the first half of the study period (1984–1996), while they did not significantly affect it in the second half. However, neighboring trees significantly affected the growth rate of trees throughout study period. Based on our findings, we speculate that an increase in sika deer population may have affected the competition between individual trees in the mixed forest. The effects of tree size and neighboring trees on mortality and growth varied depending on the growth form groups and the species.

Keywords: competition, growth form, neighboring tree, sika deer, tree size

九州大学農学部附属宮崎演習林内の針広混交林において、樹木サイズと隣接個体の胸高断面積合計が樹木の成長と枯死に及ぼす影響を、シカの個体数が増加した30年間の前期（1984-1996年）と後期（1996-2014年）とで比較した。

本調査地では下層植生が1990年代から衰退し、2000年代ではほぼ消滅した。調査期間の後期に更新した樹木のほとんどは、シカが採食しないシキミとアセビであった。小径木は成長速度が遅く、枯死率が高い傾向が調査期間を通じて観察された。調査期間の前期では、隣接個体が枯死率に有意に影響を及ぼしていたが、後期では影響が見られなかった。一方、隣接個体の成長に及ぼす影響は調査期間を通じて観察された。以上の結果から、本調査地において、シカの個体数増加は樹木の個体間競争に影響を及ぼした可能性が示唆された。これらの影響は樹木の生活型や種によって異なっていた。

キーワード：競争, 生活形, 隣接個体, シカ, 樹木サイズ

1. Introduction

Competition is a principal component of plant interactions, regulating plant communities and ecosystems (Tilman 1982; Grime 2001). For example, neighboring trees negatively influence the growth and survival of individual trees (Yoshida and Kamitani 2000; Umeki 2002; Mori and Takeda 2003). In contrast, facilitation is a positive interaction among neighboring plants that also occurs in plant communities (Callaway and Walker 1997; Kunstler et al. 2011; del Rio et al. 2014). Plant interactions can be affected by abiotic stressors such as temperature and drought (Callaway et al. 2002), as well as biotic factors such as herbivores (Rousset and Lepart 2000; Kunstler et al. 2006). In addition, plant interaction differed with changes in stand structure (Cavard et al. 2011).

Mixed conifer-broadleaf forests are widely distributed across Japan, mainly over the Pacific side of the archipelago. The forests are dominated by evergreen conifers such as *Abies firma* Sieb. et Zucc. and *Tsuga sieboldii* Carrière, and deciduous broad-leaved trees at higher elevations. Previous studies in mixed forests have

shown that there are patterns of regeneration and stand dynamics after a gap disturbance, suggesting that the competition for light resource is significant in maintaining species coexistence (Suzuki & Tsukahara 1987; Kubota 2006). However, a few researches on changes of competitive relationship between trees have conducted based on long-term monitoring in natural mixed forest (Takahashi 2010).

Populations of sika deer (*Cervus nippon*) have increased across Japan (Takatsuki 2009a) and had considerable effects on forest structure and dynamics (Akashi and Nakashizuka 1999; Tsujino and Yumoto 2004). Mixed forests in Kyushu Island, Japan has been damaged, and in severe cases, heavy browsing pressure has denuded forest floor vegetation (Murata et al. 2009a). Grime (1974) predicted that relative importance of competition for vegetation would vary along disturbance gradients. Thus, the competitive interactions between individuals may be affected by increases in sika deer populations. If heavy browsing and bark stripping reduced growth and increased mortality, the effects of the neighboring tree will decrease. On the other hand, deer may

榎木 勉・菱 拓雄・田代 直明 温帯混交林における樹木の成長と死亡に隣接個体が及ぼす影響の30年間の変化

*Corresponding author : E-mail: enoki@forest.kyushu-u.ac.jp 394 Tsubakuro, Sasaguri, Fukuoka 811-2415 Japan

¹ Division of Forest Environmental Sciences, Department of Agro-environmental Sciences, Faculty of Agriculture, Kyushu University
九州大学大学院農学研究環境農学部門森林環境科学講座

positively affect tree growth in several ways (Lucas et al. 2013). First, deer can increase nutrient input through their excretions. Second, browsing by deer may reduce understory vegetation and so reduce competition in the belowground environment. Thus, we expect the positive effects of neighbors to increase if the facilitation by deer exceeds the negative effects.

The effects of sika deer on vegetation would differ with tree species. Food habits of sika deer was variable locally with habitat variability (Takatsuki 2009b). Two evergreen broadleaf trees, *Illicium anisatum* and *Pieris japonica* subsp. *japonica* have been known as species that sika deer cannot consume in the mixed forest (Nakajima 1929). In the mixed forest, regeneration patterns were observed with growth form groups with different leaf habits—evergreen conifer, evergreen broadleaf trees and deciduous broadleaf trees (Kubota 2006). Nevertheless, no studies have investigated stand dynamics based on long-term monitoring over the entire course of the increase in a sika deer population, as it is difficult to predict and prepare for disturbance such as large increase in wild life population.

In the present study, we examined the stand dynamics of a mixed conifer-broadleaf forest for 30 years. We evaluated the effects of tree size and the basal area of neighboring trees on the growth rate and mortality of individual trees, comparing before and after sika deer population increase. We compared also the patterns of tree dynamics between different growth form groups with different leaf habits.

2. Methods

2.1 Study site

The study was conducted in a cool temperate mixed forest in the Shiiba Research Forest, Kyushu University, South-Western Japan. The forest consists of conifers such as *Abies firma* and *Tsuga sieboldii*, evergreen broad-leaved trees such as *Quercus salicina* Blume and *Quercus acuta* Thunb., and deciduous broad-leaved trees such as *Fagus crenata* Blume, *Quercus crispula* Blume and *Carpinus laxiflora* (Siebold et Zucc.) Blume. In 2002–2011, the Shiiba Research Forest Station, located 600 m a.s.l., had a recorded annual precipitation of 2,833 mm and a mean temperature of 13.1 °C. At this site, the understory has mostly been denuded by sika deer browsing in 2014. Prior to browsing, *Sasa borealis* (Hack.) Makino et Shibata covered the forest floor thickly (Murata et al. 2009a, b). Sika deer have been observed in this forest since the 1980s, and understory vegetation has decreased since the 1990s and has been denuded since the 2000s (Murata et al. 2009b; Saruki et al. 2004).

2.2 Study plot and data collection

In 1984, a study plot (30 m × 70 m) was established in the above-mentioned mixed forest at an elevation of 1100 m a. s. l. (32°24'5"N, 131°10'26"E, Aragami et al. 1987). Broad-leaved trees in and around the plot were thinned in 1978 to encourage

regeneration (Aragami et al. 1987). After thinning, the relative illumination at a height of 1 m was 60%. The diameter at breast height (DBH), height, and position of trees taller than 2 m in the plot were recorded in 1984 and 1996 (Aragami et al. 1987). We reestablished the plot in 2014 and identified the trees measured in the former study, referring to species, size and position. In 2014, we measured DBH and position of trees taller than 2 m again. We regarded the two study periods (the first and second study periods are 1984–1996 and 1996–2014, respectively) as before and after an increase in sika deer population, respectively.

2.3 Analysis

We calculated the changes in stem number (λ), the mortality rate (m), and the recruitment rate (r) of trees for the first (1984–1996) and second (1996–2014) study period following Mori et al. (2007) using the formulas:

$$\lambda = (\ln n_t - \ln n_0) / t,$$

$$m = (\ln n_0 - \ln s_t) / t,$$

$$r = (\ln n_t - \ln s_t) / t,$$

where n_0 , n_t and s_t are the number of stems at time 0 and t , and the number of stems surviving through time t , respectively. We calculated the values for all trees, the three growth form groups, and *A. firma* and *T. sieboldii*. The tree numbers of species other than *A. firma* and *T. sieboldii* were too limited for appropriate analysis. We conducted the following analyses as described above, defining the growth rate (G ; cm/year) of DBH (cm) of trees during the first and second study periods as:

$$G = (D_t - D_0) / t$$

where D_t and D_0 are the DBH of stems at time 0 and t , respectively. The difference in growth rate between the periods could not be evaluated precisely and so were not used further in this study because the position of stems at which we measured DBH in 2014 may have been different to the position at which they were measured in 1984 and 1996.

In the first and second study periods, the effects of neighboring trees were calculated using their basal area (nBA; m²), defined as:

$$\text{nBA} = \pi \sum_i (D_{0i} / 2)^2$$

where D_{0i} is the DBH(m) of the i th stem within a given radius R (2, 4, 6, 8 or 10 m) from the focal tree at time 0. We calculated the nBA as the sum of all trees within a given radius in order to examine the effects of neighboring trees. We applied the toroidal edge correction (Ripley 1979). Since light comes from above, larger plants often have an advantage in competition for light (Weiner and Thomas 1986). In the present study, however, we evaluated competition and facilitation between neighboring trees. We used the basal area of all neighboring trees to examine the effects of competition and facilitation.

To evaluate change in the contribution of competitive interactions on the stand dynamics with an increase in sika deer population, we compared the stand dynamics between the two study periods. We evaluated differences in the DBH size

distribution of trees between three censuses (1984, 1996 and 2014) using the Kolmogorov-Smirnov test. We evaluated the differences in mortality and recruitment rates between the two study periods using a Chi-square test. We analyzed the factors affecting tree growth rate and mortality using generalized linear models, assigning binomial (mortality) and Gaussian (tree growth rate) distributions, assigning tree height and BA as explanatory variables. We compared the models with different radius using Akaike's Information criteria (AIC), selecting the model with the lowest AIC value as the best model. All statistics were performed using R 3.2.1 (R Core Team 2015).

3. Results

Two evergreen conifers (*Tsuga sieboldii* and *Abies firma*) predominated in the canopy layer, while evergreen broad-leaved trees such as *Quercus salicina* and *Quercus acuta* and deciduous

broad-leaved trees, such as *Castanea crenata* Siebold et Zucc. and *Fagus crenata*, coexisted (Table 1). Tree number decreased during the first study period (1984–1996), while it increased during the second study period (1996–2014). The tree number in 1984 and 2014 were similar. The number of evergreen broad-leaved trees increased in the second study period, while those of other growth form groups decreased through the entire study period. The basal areas of all growth form groups increased through the entire study period. Especially, *Illicium anisatum* and *Pieris japonica* subsp. *japonica*, which sika deer cannot consume, increased largely in the second periods.

The frequency of trees smaller than 10cm in DBH decreased in the first study period (Kolmogorov-Smirnov test, $p < 0.05$, Fig. 1). Furthermore, the frequency of smaller evergreen conifers decreased through the entire study period ($p < 0.05$), while the frequency of evergreen broad-leaved trees smaller than 10cm

Table 1. Species composition in the study plot (70m × 30m).

| Growth form | 1984 | | 1996 | | 2014 | | |
|--|---------------------------------|--------------------|---------------------------------|--------------------|---------------------------------|--------------------|------|
| | Basal area (m ² /ha) | Stem density (/ha) | Basal area (m ² /ha) | Stem density (/ha) | Basal area (m ² /ha) | Stem density (/ha) | |
| <i>Tsuga sieboldii</i> | EC | 4.54 | 514 | 5.98 | 510 | 7.8 | 481 |
| <i>Abies firma</i> | EC | 5.85 | 195 | 8.78 | 176 | 10.58 | 143 |
| <i>Quercus salicina</i> | EB | 3.47 | 129 | 4.39 | 129 | 5.8 | 152 |
| <i>Carpinus</i> spp | DB | 1.12 | 71 | 1.72 | 76 | 1.88 | 57 |
| <i>Quercus acuta</i> | EB | 2.93 | 62 | 3.79 | 52 | 5.06 | 57 |
| <i>Quercus crispula</i> | DB | 1.73 | 62 | 1.94 | 48 | 2.63 | 48 |
| <i>Castanea crenata</i> | DB | 2.52 | 57 | 3.34 | 57 | 3.26 | 43 |
| <i>Acer</i> spp | DB | 1.01 | 33 | 1.07 | 29 | 1.41 | 38 |
| <i>Camellia japonica</i> | EB | 0.33 | 29 | 0.43 | 29 | 0.59 | 33 |
| <i>Ilex crenata</i> var. <i>crenata</i> | EB | 0.27 | 29 | 0.22 | 19 | 0 | 0 |
| <i>Fagus crenata</i> | DB | 2.17 | 19 | 2.49 | 19 | 2.75 | 19 |
| <i>Betula grossa</i> | DB | 0.4 | 19 | 0.51 | 14 | 0.56 | 14 |
| <i>Ilex pedunculosa</i> | EB | 0.21 | 19 | 0.2 | 14 | 0.26 | 19 |
| <i>Clethra barbinervis</i> | DB | 0.17 | 14 | 0.2 | 10 | 0.11 | 10 |
| <i>Neoshirakia japonica</i> | DB | 0.14 | 14 | 0.03 | 5 | 0.05 | 5 |
| <i>Cerasus jamasakura</i> | DB | 0.12 | 10 | 0.15 | 10 | 0.13 | 5 |
| <i>Quercus sessilifolia</i> | EB | 1.38 | 10 | 0.05 | 5 | 0.06 | 5 |
| <i>Ilex macropoda</i> | DB | 0.26 | 10 | 0.24 | 5 | 0.31 | 5 |
| <i>Magnolia obovata</i> | DB | 0.26 | 10 | 0.37 | 10 | 0.84 | 19 |
| <i>Eurya japonica</i> var. <i>japonica</i> | EB | 0.17 | 10 | 0.2 | 10 | 0.23 | 10 |
| <i>Illicium anisatum</i> | EB | 0.1 | 10 | 0.15 | 10 | 0.14 | 143 |
| <i>Symplocos myrtacea</i> | EB | 0.06 | 10 | 0 | 0 | 0.02 | 19 |
| <i>Pinus densiflora</i> | EC | 0.83 | 5 | 0.93 | 5 | 1.1 | 5 |
| <i>Chengiopanax sciadophylloides</i> | DB | 0.15 | 5 | 0 | 0 | 0 | 0 |
| <i>Gamblea innovans</i> | DB | 0.1 | 5 | 0 | 0 | 0 | 0 |
| <i>Lindera erythrocarpa</i> | DB | 0.06 | 5 | 0.06 | 5 | 0.05 | 5 |
| <i>Stylax japonica</i> | DB | 0.05 | 5 | 0.04 | 5 | 0 | 0 |
| <i>Lyonia ovalifolia</i> var. <i>elliptica</i> | DB | 0.04 | 5 | 0.06 | 5 | 0.09 | 5 |
| <i>Stewartia monadelpha</i> | DB | 0.01 | 5 | 0.01 | 5 | 0.01 | 10 |
| <i>Pieris japonica</i> subsp. <i>japonica</i> | EB | 0 | 0 | 0 | 0 | 0.01 | 43 |
| Evergreen Conifer | EC | 11.22 | 714 | 15.69 | 691 | 19.48 | 629 |
| Evergreen broad-leaved tree | EB | 8.92 | 308 | 9.43 | 268 | 12.17 | 481 |
| Deciduous broad-leaved tree | DB | 10.31 | 349 | 12.23 | 303 | 14.08 | 283 |
| Total | | 30.45 | 1371 | 37.35 | 1262 | 45.72 | 1393 |

EC, Evergreen conifer; EB, Evergreen broad-leaved tree; DB, Deciduous broad-leaved tree

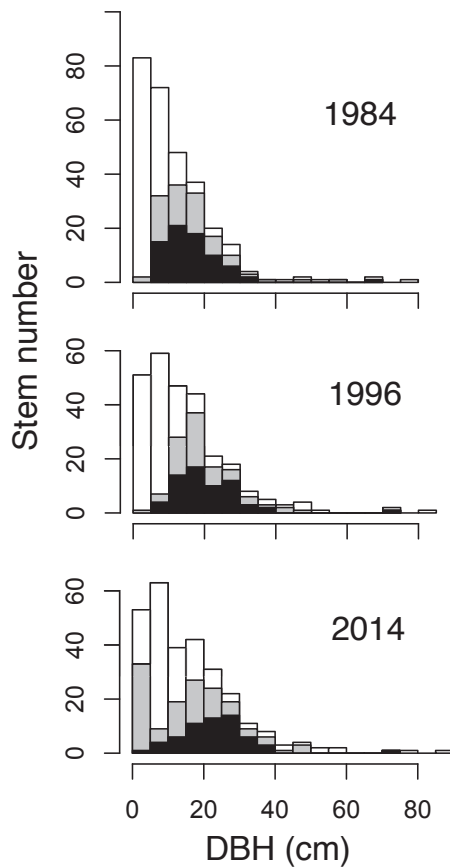


Fig. 1. Diameter at breast height (DBH) size distribution of each growth form group in 1984, 1996 and 2014 in the study plot (30m × 70m). Open area, deciduous broad-leaved trees shaded area, evergreen broad-leaved trees; filled area, evergreen conifers;

Table 2. Changes in mortality and recruitment rates of trees with study period.

| | 1984-1996 | 1996-2014 |
|------------------------|-----------|-----------|
| Mortality rate | | |
| All | 0.0142 | 0.0087 |
| EC | 0.0117 | 0.008 |
| <i>Abies firma</i> | 0.0224 | 0.012 |
| <i>Tsuga sieboldii</i> | 0.0131 | 0.0068 |
| EB | 0.0117 | 0.0102 |
| DB | 0.0135 | 0.0088 |
| Recruitment rate | | |
| All | 0.0075 | 0.0138 |
| EC | 0.0103 | 0.0034 |
| <i>Abies firma</i> | 0.0135 | 0.0019 |
| <i>Tsuga sieboldii</i> | 0.0093 | 0.0039 |
| EB | 0.0069 | 0.0366 * |
| DB | 0.0013 | 0.0077 * |

EC, Evergreen conifer; EB, Evergreen broad-leaved tree; DB, Deciduous broad-leaved tree

* significant difference between the study periods ($p < 0.05$)

in DBH increased in the second study period ($p < 0.05$), and the frequency of deciduous broad-leaved trees smaller than 10cm in DBH decreased during the first period ($p < 0.05$). The

Table 3. Differences in effects of tree DBH and basal area of neighboring trees (nBA) on the tree growth rate between the first (1984-1996) and the second (1996-2014) periods. Generalized linear model was performed for all trees, evergreen conifer (EC), evergreen broad-leaved tree (EB), deciduous broad-leaved tree (DB), *Abies firma* and *Tsuga sieboldii*. Effects in selected models with smallest AIC are shown.

| | Intercept | DBH (cm) | nBA (m ²) | R (m) |
|------------------------|-----------|-------------|-----------------------|-------|
| 1984-1996 | | | | |
| All trees | 2.75e-03 | 6.447e-2*** | -2.399e-4*** | 6 |
| EC | -3.02e-01 | -1.10e-02 | -6.93e-05 | 8 |
| <i>Abies firma</i> | -0.277 | 8.523e-2*** | -2.206e-4* | 10 |
| <i>Tsuga sieboldii</i> | -0.441 | -1.25e-02 | -6.95e-05 | 8 |
| EB | 2.15 | 9.273e-3*** | -2.890e-4** | 8 |
| DB | -0.966 | -2.43e-03 | -1.02e-04 | 8 |
| EB | -0.442 | 6.173e-2*** | -1.06e-04 | 8 |
| DB | -0.444 | -1.63e-02 | -7.12e-05 | 6 |
| EB | 3.61e-03 | 5.29e-03 | -2.18e-05 | 6 |
| DB | -7.83e-02 | -3.51e-03 | -1.33e-05 | 6 |
| DB | 1.237* | | -2.59e-05 | 6 |
| DB | -0.603 | | -1.67e-05 | 6 |
| 1996-2014 | | | | |
| All trees | -0.277 | 8.523e-2*** | -2.206e-4* | 2 |
| EC | -0.441 | -1.25e-02 | -6.95e-05 | 8 |
| <i>Abies firma</i> | 0.787 | 4.132e-2** | -2.566e-4*** | 8 |
| <i>Tsuga sieboldii</i> | -0.518 | -1.27e-02 | -6.19e-05 | 2 |
| EB | 0.386 | | | 2 |
| DB | -0.458 | | | 2 |
| <i>Tsuga sieboldii</i> | 1.370* | | -2.653e-4*** | 8 |
| EB | -0.546 | | -6.69e-05 | 8 |
| DB | -2.0186** | 8.529e-3** | | 2 |
| EB | -0.643 | -2.91e-03 | | 2 |
| DB | -2.132 | | -2.33e-05 | 8 |
| DB | -1.069 | | -1.28e-05 | 8 |

*** 0.001, ** 0.01, * 0.05

BA: the sum of basal area of all trees in radius of R (m) from the focal tree

tree mortality rates of all growth form groups, *A. firma* and *T. sieboldii* did not differ between the two study periods (Chi-square test, $p > 0.05$, Table 2). The mortality rates of *A. firma* did not differ from that of *T. sieboldii* through the entire study period ($p > 0.05$). The recruitment rate of whole trees did not differ significantly between the two study periods ($p > 0.05$). However, the recruitment rates of evergreen and deciduous broad-leaved trees increased in the second study period ($p < 0.05$), while that of evergreen conifers did not differ between the two study periods ($p > 0.05$). The recruitment rates of *A. firma* did not differ from that of *T. sieboldii* through the entire study period ($p > 0.05$).

The growth rate of whole trees in the study plot was affected positively by tree DBH and negatively by neighboring trees through the study period (Table 3). The growth rate of evergreen conifer was affected positively by tree DBH and negatively by neighboring trees through the study period. The growth rate of evergreen broad-leaved trees was positively affected by tree DBH in the second period. Tree DBH and neighboring trees did not significantly affect the growth rate of deciduous broad-leaved trees through the entire study period. In the first study period,

Table 4. Differences in effects of tree DBH and basal area of neighboring trees (nBA) on the tree mortality between the first (1984-1996) and the second (1996-2014) periods. Generalized linear model was performed for all trees, evergreen conifer (EC), evergreen broad-leaved tree (EB), deciduous broad-leaved tree (DB), Effects in selected models with smallest AIC are shown.

| | Intercept | DBH (cm) | nBA (m ²) | R (m) |
|------------------------|-----------|--------------|-----------------------|-------|
| 1984-1996 | | | | |
| All trees | -4.442*** | -7.792e-2** | 1.154e-4* | 10 |
| | -0.6174 | -2.58e-02 | -5.74e-05 | |
| EC | -4.457*** | -2.902e-1** | 2.047e-4* | 10 |
| | -0.939 | (1.016e-0.1) | | |
| <i>Abies firma</i> | -2.810. | -0.372* | 2.413e-4. | 10 |
| | -1.495 | -0.177 | -1.36e-04 | |
| <i>Tsuga sieboldii</i> | -4.425** | -0.525** | 2.368e-4* | 10 |
| | -1.421 | -0.203 | -1.12e-04 | |
| EB | -4.295*** | | | |
| | -0.356 | | | |
| DB | -2.881 | -0.08 | | |
| | -0.869 | -0.056 | | |
| 1996-2014 | | | | |
| All trees | -3.620*** | -8.634e-3** | | |
| | -0.329 | -2.70e-03 | | |
| EC | -4.575*** | -0.186* | 1.02e-04 | 10 |
| | -0.962 | -8.40e-02 | (6.508-5) | |
| <i>Abies firma</i> | -0.681 | -0.355* | | |
| | -1.309 | -0.166 | | |
| <i>Tsuga sieboldii</i> | -7.557*** | -0.240. | 3.018e-5* | 10 |
| | -1.552 | -0.129 | -1.08e-05 | |
| EB | 3.383 | -6.373e-4* | -4.21e-05 | 8 |
| | -2.7 | -2.97e-04 | -2.99e-05 | |
| DB | -1.812 | -2.622e-4* | 9.91e-05 | 2 |
| | -1.283 | -1.12e-04 | -6.68e-05 | |

*** 0.001, ** 0.01, * 0.05, . 0.01

BA: the sum of basal area of all trees in radius of R (m) from the focal tree

the growth rate of *A. firma*, was positively affected by tree DBH and negatively by neighboring trees. On the other hand, in the second period, the growth rate of *A. firma* was not affected by the DBH and neighboring trees. In the first study period, growth rate of *T. sieboldii* was positively affected by tree DBH, while it was negatively affected by neighboring trees in the second period.

The mortality of whole trees in the study plot was negatively affected by tree DBH and positively by neighboring trees in the first study period, while it was affected only by tree DBH in the second period (Table 4). The relationship of the mortality of evergreen conifer to tree DBH and neighboring trees was similar to that of whole trees through the entire study period. The mortality of evergreen broad-leaved trees was negatively affected by tree DBH in the second study period. Through the entire study period, neighboring trees did not significantly affect the mortality of deciduous broad-leaved trees, while tree DBH did affect mortality in the second study period. The mortality of *A. firma* was negatively affected by tree DBH and positively by neighboring trees in the first period, while it was affected only by tree DBH in the second period. The mortality of *T. sieboldii* was

negatively affected by tree DBH and positively by neighboring trees through the entire study period.

4. Discussion

Stand dynamics in the mixed forest differed between two study periods. Although the mortality and recruitment rates of whole trees did not differ during the entire study period (1984–2014), stem density decreased in the first study period (1984–1996), and increased in the second (1996–2014). The decrease in stem density in the first study period was mainly due to a decrease in small trees, suggesting that the decrease in stem density might be a result of competition between individuals. On the other hand, the increase in stem density in the second study period was mainly due to a decrease in tree mortality and an increase in recruitment of species that sika deer cannot consume, such as *Illicium anisatum* and *Pieris japonica* subsp. *japonica* (Nakajima 1929). We observed the recruitment of inedible tree species only in the second study period. Based on our results, we suggest that the competition between individuals in the previous period and the effects of sika deer in the latter period may create niches that allow regeneration of tree species that sika deer cannot consume. We discuss the possible mechanisms of the change in the stand dynamics below.

The effect of neighboring trees on the mortality of whole trees in the study plot was significant in the first study period, but not in the second. In contrast, the effect of neighboring trees on the growth of whole trees was significant through the entire study period. These effects of neighboring trees suggest that competition between individual trees has occurred through the entire study period, but did not affect mortality in the second study period. The high mortality of smaller trees in the second study period could be partly due to sika deer. Small trees are likely to be damaged by sika deer bark stripping (Akashi and Nakashizuka 1999; Suzuki et al. 2011).

The mixed forest consisted of three growth form groups: evergreen conifer; evergreen broad-leaved trees; and deciduous broad-leaved tree, the composition of which has varied over 30 years. The effects of tree size and neighboring trees on mortality and growth of trees varied depending on growth form groups and species. Evergreen conifers, predominant in the plot, showed a similar pattern to that of whole trees in the plot. Neighboring trees had significant effects on mortality in the first study period, but not in the second, though neighboring trees did significantly affect growth through the entire study period. The two predominant species, *A. firma* and *T. sieboldii*, had different patterns of tree dynamics. The difference in shade tolerance between *A. firma* and *T. sieboldii* may explain this difference. Neighboring trees significantly affect the mortality of the less shade-tolerant *T. sieboldii* (Nakao 1985; Suzuki and Tsukahara 1987), but not on those of the more shade-tolerant *A. firma*. On the other hand, we did not find reasons for that neighboring trees

had a significant effect on growth of *A. firma* and *T. sieboldii* in the first and second study period, respectively.

Neighboring trees did not significantly affect the mortality and growth of evergreen and deciduous broad-leaved trees, while tree DBH did. These findings suggest that evergreen and deciduous broad-leaved trees were unlikely to be affected by competition with neighboring trees. However, in the study plot, many different species of evergreen and deciduous broad-leaved trees were present, in contrast to evergreen conifers, which were represented by fewer species. Different species could have different patterns of tree dynamics as *A. firma* and *T. sieboldii* showed different patterns. Especially, evergreen broad-leaved trees include species that sika deer cannot consume. Based on these results, we examined the possibility that an increase in sika deer population may have affected the competition between individual trees in a cool temperate mixed forest, though we cannot explicitly extract the effects of sika deer from results of the tree census. Experiments such as enclosure and population control are available to evaluate the change in the contribution of competitive interactions and the increases in the sika deer population.

Species composition and stand structure of the mixed forests varies depending on climate, topography, and anthropogenic factors (Nakao 1985). The surroundings of the study site had been thinned partially to enhance regeneration by improving the light conditions (Aragami 1987). The basal area of 30.5 m²/ha in 1984 was considerably smaller than that of other neighboring mixed forests (c.a. 80 m²/ha, Aragami 1987; Okano and Aragami 1999). The increase in basal area through the entire study period indicates biomass recovery as a result of thinning. However, the basal area of 45.7 m²/ha was still smaller than those of other neighboring mixed forests. Growth of standing trees and recruitment of trees that sika deer cannot consume would further increase the basal area in the study plot. Further research on each species would confirm our prediction and results regarding evergreen and deciduous broad-leaved trees.

Acknowledgements

This study was conducted following previous work in the Shiiba Research Forest (SRF), Kyushu University directed by Dr. Aragami. We thank Shiiba Y, Kubota K, Kaji K, Cho K, Yamauchi K, Ogata T and other staff of SRF for their help on the field survey.

Data accessibility

Data used in this study can be accessed through Kyushu University Forests Data Archive: <http://www.forest.kyushu-u.ac.jp/data-archive/index.php?2017001>

References

Akashi N, Nakashizuka T (1999) Effects of bark-stripping by Sika deer (*Cervus nippon*) on population dynamics of a

mixed forest in Japan. For Ecol Mange 113: 75-82. doi: 10.1016/S0378-1127(98)00415-0

Aragami K (1987) Studies on the process of formation of *Abies* and *Tsuga* natural forest in the central mountain district of Kyushu (in Japanese with English summary). Bull Kyushu Univ For 57: 17-108.

Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002) Positive interactions among alpine plants increase with stress. Nature 417: 844-848. doi:10.1038/nature00812

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965. doi:10.1890/0012-9658(1997)078[1958:-CAFASA]2.0.CO;2

Cavard X, Bergeron Y, Chen HYH, Paré D, Laganière J, Brassard B (2011) Competition and facilitation between tree species change with stand development. Oikos 120: 1683-1695. doi:10.1111/j.1600-0706.2011.19294.x

del Rio M d, Scütze G, Pretzsch H (2014) Temporal variation of competition and facilitation in mixed species forests in Central Europe. Plant Biol 16: 166-176. doi:10.1111/plb.12029

Grime JP (1974) Vegetation classification by reference to strategies. Nature 250: 26-31. doi:10.1038/250026a0

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons, New York

Kubota Y (2006) Spatial pattern and regeneration dynamics in a temperate *Abies-Tsuga* forest in southwestern Japan. J For Res 11: 191-201. doi:10.1007/s10310-006-0205-z

Kunstler G, Curt T, Bouchaud M, Lepart J (2006) Indirect facilitation and competition in tree species colonization of sub-Mediterranean grasslands. J Veg Sci 17: 379-388. doi:10.1658/1100-9233(2006)017[0379:IFACIT]2.0.CO;2

Kunstler G, Albert CH, Courbaud B, Lavergne S, Thuiller W, Vieilledent G, Zimmermann NE, Coomes D (2011) Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients. J Ecol 99: 300-312. doi:10.1111/j.1365-2745.2010.01751.x

Lucas RW, Salguero-Gómez R, Cobb DB, Waring BG, Anderson F, McShea WJ, Casper BB (2013) White-tailed deer (*Odocoileus virginianus*) positively affect the growth of mature northern red oak (*Quercus rubra*) trees. Ecosphere 4: 1-15. doi:10.1890/ES13-00036.1

Mori A, Takeda H (2003) Light-related competitive effects of overstory trees on the understory conifer saplings in a subalpine forest. J For Res 8: 163-168. doi:10.1007/s10310-002-0022-y

Mori AS, Mizumachi E, Komiyama A (2007) Roles of disturbance and demographic non-equilibrium in species coexistence, inferred from 25-year dynamics of a late-suc-

- cessional old-growth subalpine forest. For Ecol Manage 241: 74-83. doi:10.1016/j.foreco.2006.12.031
- Murata I, Saruki S, Kubota K, Inoue S, Tashiro N, Enoki T, Utsumi Y, Inoue S (2009a) Effects of sika deer (*Cervus nippon*) and dwarf bamboo (*Sasamorpha borealis*) on seedling emergence and survival in cool-temperate mixed forests in the Kyushu Mountains. J For Res 14: 296-301. doi:10.1007/s10310-009-0131-y
- Murata I, Inoue S, Yabe T, Kabemura Y, Kaji K, Kubota K, Mabuuchi T, Shiiba Y, Utsumi Y (2009b) Sika deer density and vegetation changes for 37 years in Shiiba Research Forest (in Japanese with English summary). Bull Kyushu Univ For 90: 13-24.
- Nakajima M (1929) The feeding experiments of Japanese deer in the University Forest in Chiba prefecture (in Japanese). Bull Univ of Tokyo For 8: 95-114.
- Nakao T (1985) Ecological studies of *Abies* and *Tsuga* forests in Kyushu, Japan (in Japanese with English summary). Bull Miyazaki Univ Forest 11: 1-165.
- Okano T, Aragami K (1999) Changes in the stand structure during a 12-year period in a natural Fir-Hemlock forest in mountain region of Kyushu (in Japanese with English summary). J Jpn For Soc 81: 1-9.
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Ripley BD (1979) Test of 'randomness' for spatial point patterns. J Royal Stat Soc B 41: 368-374
- Rousset O, Lepart J (2000) Positive and negative interactions at different life stages of colonizing species (*Quercus humilis*). J Ecol 88: 401-412. doi:10.1046/j.1365-2745.2000.00457.x
- Saruki S, Inoue S, Shiiba Y, Nagasawa H, Ohsaki S, Kubota K (2004) Distribution and growth situation of Suzutake (*Sasamorpha borealis*) damaged by grazing of Sika deer (*Cervus nippon nippon*) in Miyazaki Forest of Kyushu University: case study in 2003 (in Japanese with English summary) Bull Kyushu Univ For 85: 47-54.
- Suzuki E, Tsukahara J (1987) Age structure and regeneration of old growth *Cryptomeria japonica* forests on Yakushima Island. Bot Mag Tokyo 100: 223-241. doi:10.1007/BF02492832
- Suzuki M, Fujiwara A, Kamoda S, Maehara T, Saito H, Matsui M, Iguchi K, Kaji M, Kamata N (2011) Factors affecting the probability of bark-stripping by deer in a natural forest: an analysis based on tree characteristics, deer habitat utilization and environmental conditions (in Japanese with English summary). J Jpn For Sci 93: 213-219.
- Takahashi K (2010) Effects of altitude and competition on growth and mortality of the conifer *Abies sachalinensis*. Ecol Res 25: 801-812. doi:10.1007/s11284-010-0710-6
- Takatsuki S (2009a) Effects of sika deer on vegetation in Japan: A review. Biol Conserv 142: 1922-1929. doi:10.1016/j.biocon.2009.02.011
- Takatsuki S (2009b) Geographical variations in food habits of sika deer: the northern grazer vs. the southern browser. In McCullough DR, Takatsuki S, Kaji K (eds) Sika Deer: Biology and Management of Native and Introduced Populations. Springer, Tokyo, pp 231-237
- Tilman D (1982) Resource competition and community structure. Princeton University press, Princeton, New Jersey, 296 pp
- Tsujino R, Yumoto T (2004) Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. Ecol Res 19: 291-300. doi:10.1111/j.1440-1703.2004.00638.x
- Umeki K (2002) Tree mortality of five major species on Hokkaido Island, northern Japan. Ecol Res 17: 575-589. doi:10.1046/j.1440-1703.2002.00516.x
- Weiner J, Thomas SC (1986) Size variability and competition in plant monocultures. Oikos 47: 211-222. doi:10.2307/3566048
- Yoshida T, Kamitani T (2000) Interspecific competition among three canopy-tree species in a mixed-species even-aged forest of central Japan. For Ecol Manage 137: 221-230. doi:10.1016/S0378-1127(99)00330-8

(2017年9月29日受付 : 2018年1月19日受理)