


Article

Bark Stripping by Deer Was More Intensive on New Recruits than on Advanced Regenerants in a Subalpine Forest

Takuo Nagaike 

Yamanashi Forest Research Institute, Forest Research Division, Saisyoji 2290-1, Fujikawa, Yamanashi 400-0502, Japan; nagaike-zty@pref.yamanashi.lg.jp

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Abstract: Research Highlights: To ensure sustainable forest regeneration, it is important to clarify whether new recruits or advanced regenerants are more likely to be stripped. Therefore, the effects of bark stripping on saplings in subalpine forests with abundant saplings should be analyzed by regeneration mode, but there have been no such studies until now. Background and Objectives: I investigated the effects of bark stripping by *Cervus nippon* on saplings in a subalpine coniferous forest in central Japan to (1) reveal differences in bark stripping between new recruits and advanced regenerants and (2) clarify the factors affecting survivorship. Materials and Methods: A 50 m × 140 m (0.7 ha) plot was set in the old-growth subalpine coniferous forest. All trees in the plot that were ≥2 m in height were tagged, identified to species, measured diameter at breast height and recorded bark stripping by deer. These trees and new recruits were counted and measured in 2005, 2007, 2012, and 2017. I compared saplings recruited in 2007, 2012, and 2017 (“new recruits”) with existing saplings of the same size (“advanced regenerants”). Results: The density of new recruits of *Abies mariesii* and *Tsuga diversifolia* increased, whereas that of *Abies veitchii* decreased. The proportion of stripped saplings was greater in new recruits than in advanced regenerants, significantly so in *A. veitchii*, which also had the highest maximum bark stripping ratio. Factors affecting the survivorships applied by the regression tree analysis were the maximum stripping ratio of stems for the two *Abies* species and the initial size for the *T. diversifolia*. Conclusions: Bark stripping by deer was more intensive on new recruits than on advanced regenerants in a subalpine forest, and regeneration in canopy gaps might fail because of intensive bark stripping in areas overabundant in deer.

Keywords: debarking; Mt. Fuji; mortality; regeneration; sika deer

1. Introduction

In Japan, hunting for sika deer (*Cervus nippon*) was banned before 1950s, because deer abundance was declined due to overexploitation [1,2]. Sika deer abundance was sharply increasing from 1970s and possibly explanation of the population growth was decline of snow by global warming to reduce fawn mortality, decline of number of hunters and abandonment of agricultural field by depopulation in countryside [1]. As a result, sika deer overabundant caused severe damage in agricultural, forestry and natural ecosystems in Japan.

Overabundant deer cause serious issues for forest ecosystems by limiting the regeneration of natural forests [3–5], damaging planted trees [6–10], and consequently altering the species composition, stand structure, and ecosystem functions of forests [11,12]. These issues are caused mainly by foraging behaviors: stripping of bark from saplings and trees [13–15] and browsing on those and understory vegetation [16–18]. Bark stripping greatly damages saplings and trees by destroying xylem water

conductivity [19] and increasing fungal infection [13]. In some areas overabundant in deer, such as central Japan, deer affect saplings and trees much more by bark stripping than by browsing [8,14,15,20].

Subalpine forests regenerate in part through the formation of small gaps in the canopy, which other trees then fill (e.g., [21–23]). Regeneration in subalpine coniferous forests is characterized by small spatial scales (mean gap size in Japan is about 40 m², [21]) and by rich advanced regeneration beneath canopy trees [22,24].

Studies of bark stripping by deer revealed that the size dependency of preferred species depends on deer abundance [2,25–27]. Some studies showed that smaller saplings and trees were commonly stripped [7,9,10,28]. Thus, in a forest with abundant saplings, saplings would be stripped more than large trees. In subalpine coniferous forests, new recruits and advanced regenerants of the same size, but with different ecological functions, occur together. New recruits appear in good light conditions allow them to grow steadily until they achieve canopy closure. Advanced regenerants have already grown beneath the canopy and wait for gaps to be created, and then grow after canopy gap creation to become canopy trees [21]. Thus, saplings of both generation modes are important in sustaining forest dynamics. To ensure sustainable forest regeneration, it is important to clarify whether new recruits or advanced regenerants are more likely to be stripped. Therefore, the effects of bark stripping on saplings in subalpine forests with abundant saplings should be analyzed by regeneration mode, but there have been no such studies until now.

Deer are attracted to rich forage sites with better light [29]. Therefore, browsing and bark stripping would be more common in gaps than under the closed canopy. Several studies have reported the relationship between canopy condition and deer browsing in relation to gap size partitioning and fencing effects [30–35], but few studies have considered bark stripping [5,25]. Survivorship of stripped trees is affected by interactions of stripped area, competition, and tree size [13]. Thus, studies of bark stripping in a subalpine forest with abundant saplings should include such factors and regeneration mode.

Here, I investigated the effects of bark stripping by deer on saplings in a subalpine coniferous forest in central Japan and answer the following questions: (1) are there any differences in bark stripping between new recruits and advanced regenerants and (2) what factors affecting survivorship?

2. Materials and Methods

2.1. Study Site

The study was conducted in a subalpine zone on the northern slope of Mt. Fuji, central Japan (2100 m above sea level [a.s.l.]; 35°22' N, 138°41' E). At the nearest meteorological station (Kawaguchiko; 860 m a.s.l.) the mean annual precipitation was approximately 1600 mm and the mean annual temperature was 10.6 °C. Snow cover at the site was usually 50 cm from December to April.

Most of the area was covered by old-growth forests, typically dominated by *Abies mariesii*, *Abies veitchii*, and *Tsuga diversifolia* [24,36]. Some sections of the forest were disturbed by a road built around 50 years ago, whereas other parts retained their old-growth state [37]. The understory of subalpine coniferous forests in Japan is classified as herb, dwarf bamboo, or moss type [24]; the study forest is the moss type. The estimated density of sika deer, which strip bark in this area, increased sharply from 1.4/km² in 2005 to 55.1/km² in 2012 [38]. In the study area, coniferous tree species had been stripped but not heavily browsed by sika deer [8,15,20], in contrast to other regions (e.g., [17,31,39,40]). The study site is described in detail by Nagaike [15,37].

Seasonal migration of sika deer in the study area is unclear, but that would be towards safer area avoiding hunting and culling and warm and less snowy area in winter [41,42]. Jiang et al. [8] showed that the seasonal peak of bark stripping in *A. veitchii* plantations in 1500 m a.s.l. at Mt. Fuji was March–April because sika deer needs more nutrition and easily digested food due to increased nutrient demands. Forest floor in the study stand (2100 m a.s.l.) in March–April is covered by snow, but sika deer often observed on the snow by camera trapping in Yamanashi prefecture and could approach to the saplings of coniferous trees. Thus, sika deer might bark stripped from late spring to early summer.

2.2. Field Study

In 1999, a 50 m × 140 m (0.7 ha) plot was set in the old-growth subalpine coniferous forest. The canopy layer was composed of only three evergreen coniferous tree species: *A. mariesii*, *A. veitchii*, and *T. diversifolia* [37]. The plot was divided into 280 cells of 5 m × 5 m. In 1999, all trees in the cells that were ≥2 m in height were tagged and identified to species. Their diameter at breast height (DBH; 1.3 m) was measured. These trees and new recruits were counted and measured in the summer in 2005, 2007, 2012, and 2017. I compared saplings recruited in 2007, 2012, and 2017 (“new recruits”) with existing saplings of the same size (“advanced regenerants”), because bark stripping has size dependency (see Results). The three species have high shade tolerant ability and both regeneration mode.

The degree of bark stripping visible on each tree was recorded in 2007, 2012, and 2017 as the proportion of the tree circumference that had been stripped at a given height, in increments of 10%. This proportion is referred to as the bark stripping ratio (SR). A 100% SR indicated that deer had stripped all of the bark from the circumference.

2.3. Analysis

I analyzed two periods (2007–2012 and 2012–2017). Because most trees suffered repeated stripping [15,43], I determined the maximum bark stripping ratio (MSR) of each tree during each period. Survivorship ratio was calculated as the ratio of the number of the end of the census period to the number of stems alive at the beginning of the study in each study period. To analyze the effects of canopy condition and tree competition (i.e., shading and crowding) on focal saplings, I used the total cumulative basal area, as an index of canopy condition and competition, in the cell where a focal saplings located, as a competition index (CI). The reason why I chose the total cumulative basal area as CI was described in detail in Nagaike [15].

The CI was compared between new recruits and advanced regenerants by using the asymptotic Wilcoxon signed-rank test. The ratio of the number of stripped saplings to the total number of focal saplings and the survivorship ratio of the focal saplings of each species were compared between regeneration modes by using the exact Wilcoxon signed-rank test.

To identify factors affecting the survivorship of the focal saplings (i.e., the size of the focal saplings, regeneration mode, MSR, and CI), I used recursive partitioning and regression tree analysis [44]. This analysis uses a binary recursive partitioning approach to split the data set into subsets based on explanatory variables chosen to minimize the deviance in the response variables in each of the resulting subsets. The survivorship of each focal sapling in each study period is the response variable. As explanatory variables I used the DBH in the earlier year (i.e., 2007 for 2007–2012 and 2012 for 2012–2017), the CI in the later year (i.e., 2012 for 2007–2012 and 2017 for 2012–2017), the MSR, and regeneration mode. Since allowing the regression tree to grow unpruned will result in an overfitted model as noise is fitted along with data [45], I used a complexity parameter for pruning splits in each analysis.

All statistical analyses were performed in R [46], and the regression tree analysis was performed in the “rpart” package [44].

3. Results

3.1. Stand Structure

Bark stripping was biased to smaller size classes of saplings of each species (Figure 1). The numbers of trees of each species in smaller classes decreased sharply over time, particularly in *A. veitchii*, although some *A. veitchii* trees reached larger size classes. The density of new recruits of *A. mariesii* and *T. diversifolia* increased from 2007 to 2017, but that of *A. veitchii* decreased (Table 1).

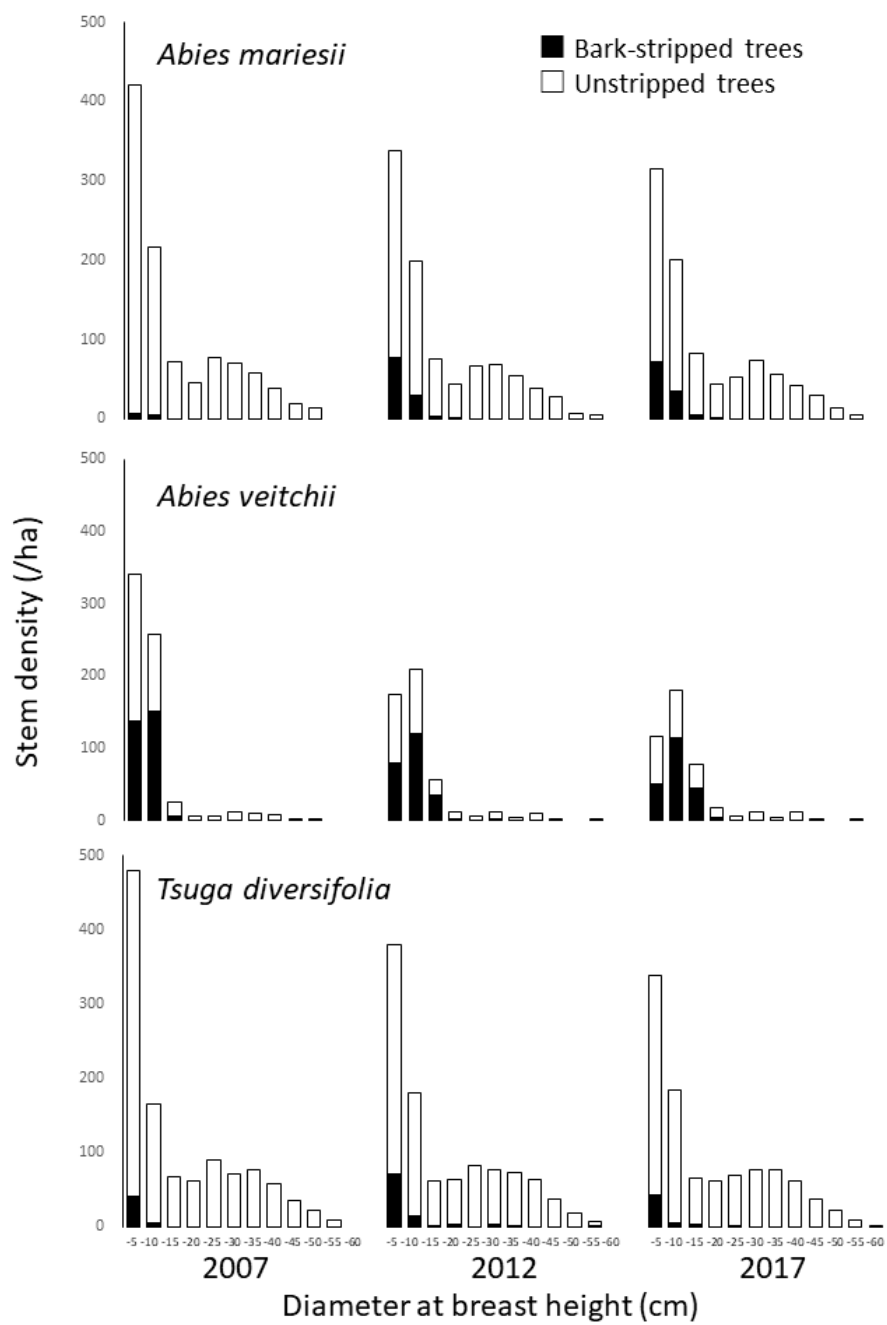


Figure 1. Diameter at breast height distribution of the three conifer species.

Table 1. Size and density of new recruits.

Species		DBH (cm)			Density (/ha)
		Min	Median	Max	
<i>Abies mariesii</i>	2007	1.3	2.2	3.7	12.9
	2012	1.6	2.4	3.2	28.6
	2017	1.5	2.7	6.0	50.0
<i>Abies veitchii</i>	2007	0.4	2.1	4.1	22.9
	2012	1.3	2.3	3.2	14.3
	2017	1.4	2.7	5.7	12.9
<i>Tsuga diversifolia</i>	2007	0.1	1.2	5.5	18.6
	2012	0.7	1.7	3.4	25.7
	2017	1.1	1.7	5.3	30.0

The cumulative basal area of new recruits was smaller than that of advanced regenerants, indicating that the new recruits were located beneath sparse canopy with less competition and better light (Table 2).

Table 2. Comparisons of cumulative basal area in each cell where saplings grew, as a competition index (CI).

Species		New Recruits			Advanced Regenerants			Asymptotic Wilcoxon Signed-Rank Test
		Mean (m ² /ha)	SD	Density (/ha)	Mean (m ² /ha)	SD	Density (/ha)	
<i>Abies mariesii</i>	2007–2012	50.3	45.6	12.9	57.3	39.8	241.4	$p < 0.001$
	2012–2017	51.8	41.5	28.6	61.8	33.9	97.1	$p < 0.001$
<i>Abies veitchii</i>	2007–2012	36.4	28.3	22.9	61.2	33.1	224.3	$p < 0.001$
	2012–2017	64.9	27.5	14.3	64.9	35.3	64.3	$p < 0.001$
<i>Tsuga diversifolia</i>	2007–2012	52.5	31.8	18.6	58.3	34.0	485.7	$p < 0.001$
	2012–2017	51.9	34.6	25.7	61.0	35.3	204.3	$p < 0.001$

3.2. Bark Stripping

In 2017, the proportion of stripped saplings was greater in new recruits than in advanced regenerants, significantly so in *A. veitchii* (Figure 2). In *A. mariesii*, it was higher in advanced regenerants in 2012 but in new recruits in 2017 (Figure 2). In *T. diversifolia*, it was significantly higher in new recruits in 2012. MSR was significantly larger in new recruits and was highest, at 47.1%, in *A. veitchii* in 2007–2012 (Table 3).

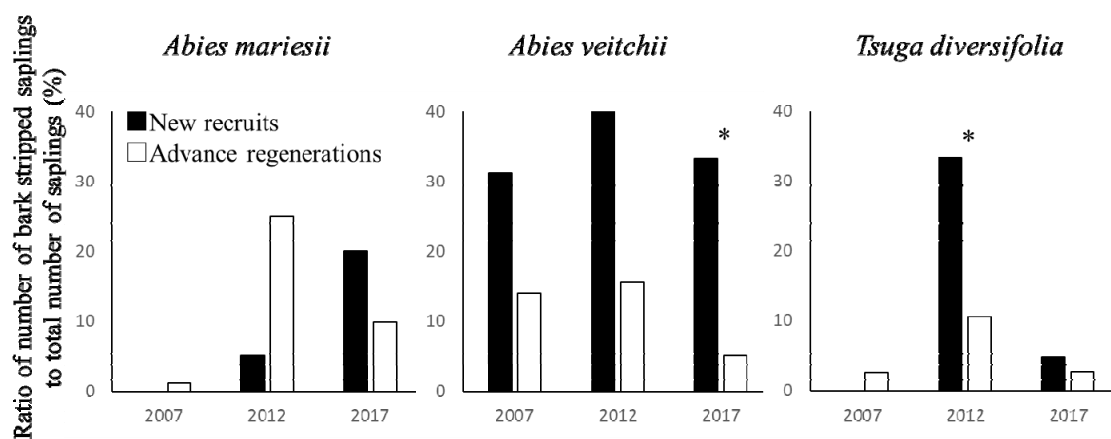
**Figure 2.** Ratios of number of stripped saplings to total number of saplings. *: $p < 0.05$.

Table 3. Comparisons of maximum bark stripping ratio between new recruits and advanced regenerants (%).

Species		New Recruits		Advanced Regenerants		Exact Wilcoxon Signed-Rank Test
		Mean	SD	Mean	SD	
<i>Abies mariesii</i>	2007–2012	33.3	43.3	21.8	35.4	$p < 0.001$
	2012–2017	16.8	31.6	22.8	33.7	$p < 0.001$
<i>Abies veitchii</i>	2007–2012	47.1	32.0	33.9	38.1	$p < 0.001$
	2012–2017	43.3	25.5	24.9	31.4	$p < 0.001$
<i>Tsuga diversifolia</i>	2007–2012	13.3	29.6	9.2	22.1	$p < 0.001$
	2012–2017	30.0	39.4	10.0	23.6	$p < 0.001$

MSR was larger in *A. veitchii* than in *A. mariesii* and *T. diversifolia*. Survivorship did not differ significantly between new recruits and advanced regenerants (Figure 3). Separating the first node of the regression tree analysis of the two *Abies* species in both study periods at their MSR (Figure 4a,b) and that of *T. diversifolia* at initial size revealed the factors affecting the survivorship of saplings of each species (Figure 4c). The CI was not selected in the models.

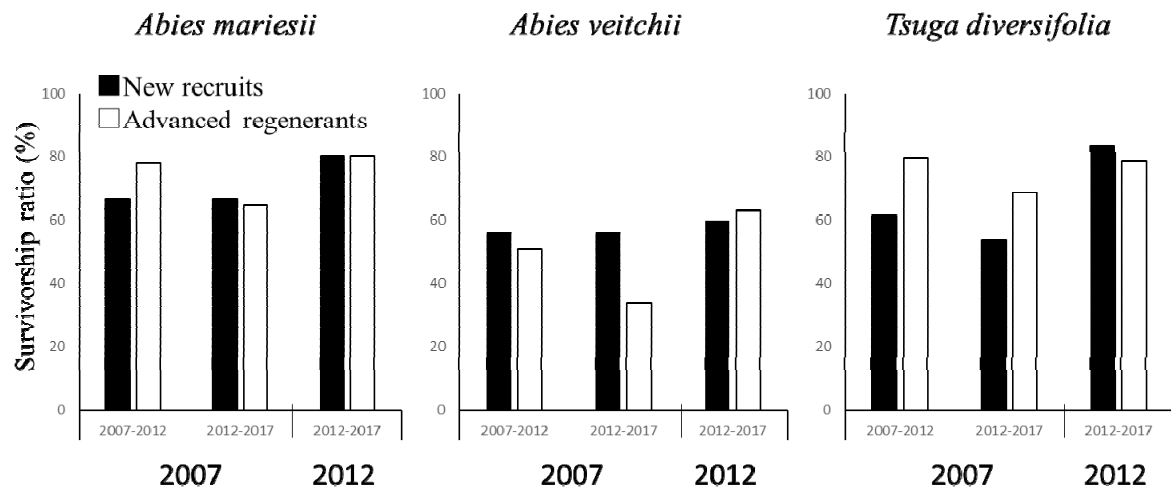


Figure 3. Survivorship ratios of new recruits and advanced regenerants. For saplings living in 2007, the survivorship ratios of new recruits and advanced regenerants of the same size as the new recruits in 2007–2012 and 2012–2017 are shown. For saplings living in 2012, the survivorship ratios of gap successors and advanced regenerants of the same size as the new recruits in 2012–2017 are shown. No differences between new recruits and advanced regenerants were significant.

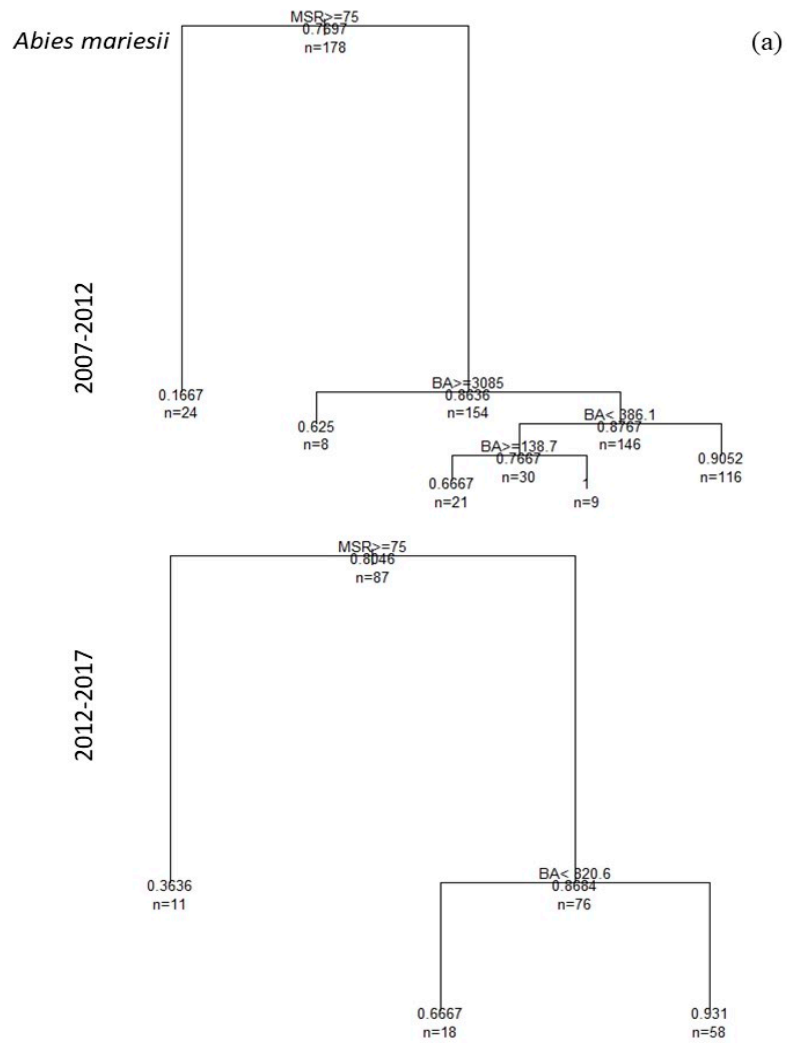


Figure 4. Cont.

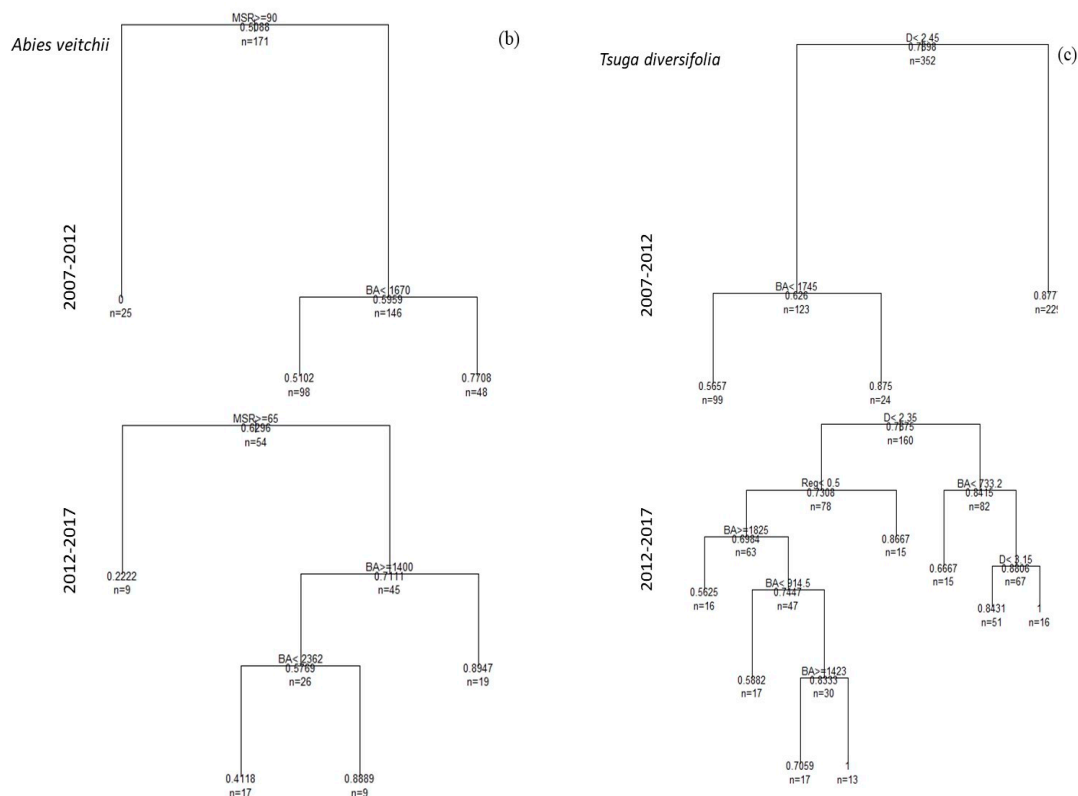


Figure 4. Results of tree regression models drawn to clarify the factors affecting survivorship of saplings of the three conifer species. At the first node, the first line gives the most influential factor affecting the survival and the threshold values. Threshold values of the explanatory variables recursively divide the data into homogeneous clusters at each node, according to whether they meet the criterion (death to the left and survive to the right). MSR—maximum bark stripping ratio; BA—basal area; D—diameter at breast height; Reg—regeneration mode. (a) *Abies mariesii*, (b) *Abies veitchii*, (c) *Tsuga diversifolia*.

4. Discussion

4.1. Effects of Regeneration Mode on Bark Stripping

New recruits can reach the canopy because of good light and low competition in gaps [21], but gaps can attract ungulate herbivores because of the rich forage [29]. Thus, gaps have positive effects on resources essential for tree growth but negative effects on survival through competition and browsing [30]. Here, new recruits were stripped more than advanced regenerants (Figure 2; Table 3), although saplings of suitable size for bark stripping were more abundant among advanced regenerants (Figure 1; Table 1). Walters et al. [32] showed that shrub-herb vegetation increased with canopy gap size and decreased deer browsing on tree seedlings by being more attractive for foraging. Here, since the understory vegetation was sparse even in better light conditions because of the moss-type understory [24], bark stripping of saplings would be concentrated on new recruits.

Migration of sika deer was affected with not only food sources but also human interactions. For example, in hunting season (November–March), sika deer has avoided hunting area even in suitable foraging sites (e.g., pastures) and moved to safer sites even with poor forage (e.g., forested areas prohibited the hunting) [41]. Main forage of sika deer was usually grass and forbs [1]. In the study forest, those plants were originally scarce, thus deer would eat bark of subalpine trees from late spring to early summer.

New recruits were stripped more than advanced regenerants (Figure 2), although survivorship did not differ significantly (Figure 3) and the regeneration mode was not a significant factor in the regression tree analysis (Figure 4). MSR in part determined the survivorship of saplings of both

Abies species: saplings were likely to die if MSR was >75% in *A. mariesii* in both study periods; >90% in *A. veitchii* in 2007–2012 and >65% in 2012–2017 (here); and >80% in *A. veitchii* [15]. In *A. veitchii*, MSR was lower in 2007–2012 than in 2012–2017, indicating that fewer saplings might have been sensitive to mortality due to bark stripping in 2007–2012. Thus, the intensity of bark stripping of individual stems is important for their survivorship, regardless of regeneration mode.

4.2. Species Preference for Bark Stripping

Factors affecting the survival of saplings differed between species: deer effects for *Abies* species but initial size for *T. diversifolia*, reflecting susceptibility to competition effects (Figure 4). This difference could alter the future species composition if deer effects were to continue. Survivorship of *T. diversifolia* saplings was affected by stem size (Figure 4): smaller saplings were more likely die; the explanation is that fewer *T. diversifolia* trees were stripped than *Abies* trees [15] and MSR is higher in *Abies* species (Table 3). Species preference for bark stripping [47,48] is explained mainly by bark chemical and nutrient contents [8,49–52], bark physical properties [51,53], and stem morphology [39]. Why the *Abies* species were preferred to *T. diversifolia* is not clear, but other studies in central Japan showed the same result [14,20].

The number of new recruits of *A. veitchii* decreased over time (Table 1) because of greater bark stripping of this species (Figure 2; Table 3). This result indicates that bark stripping by sika deer could reduce the survivorship and growth of new recruits (Table 2) and limit regeneration in this forest, particularly by *A. veitchii*. Stand structure and species composition have been changing, particularly through the reduction of tree recruitment [10,33,54]. The number of canopy trees was stable in the study period (Figure 1) because of the absence of major disturbance (e.g., windthrow), but that of saplings decreased sharply, particularly *A. veitchii*. If canopy decline were to occur in the future [31], a lack of saplings, particularly new recruits, would compromise stand structure and alter species composition in the forest.

5. Conclusions

The sharply increasing number of bark stripped trees [15] would be reflected by the increasing number of sika deer. The dramatic increase of deer density could lead to food shortage and might change their food habit from forbs and grass to tree bark. Species preferred by deer for bark stripping and browsing may fail to regenerate, and consequently canopy species composition might change through the decline of such species [18,31,54]. New recruits—saplings that respond to improvements in light in the understory—are important to forest dynamics. This study showed stronger effects of bark stripping on those than on advanced regenerants. Therefore, studies of forest dynamics in areas where deer are overabundant must focus on the effects of deer among multiple agents of disturbance [31,55]. In forests where deer are overabundant, fencing or attaching tree guards could be necessary to ensure regeneration.

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