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## Dynamics of dwarf bamboo populations and tree regeneration over 40 years in a clear-cut beech forest: effects of advance weeding and herbicide application

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### ABSTRACT

We explored the dynamics of dwarf bamboo populations in a beech forest 11 years before and 30 years after clear-cutting. Repeated weeding or herbicide application (sodium chlorate) was used experimentally to reduce or eliminate dwarf bamboo prior to clear-cutting. At the beginning of the study, the understory comprised dense populations of two *Sasa* species, the dominant *S. palmata* and the less common *S. kurilensis*. Both weeding and herbicide application rapidly reduced the cover of *S. palmata*, but it began to recover prior to clear-cutting and soon exceeded initial cover values. Both weeding and herbicide application reduced the cover of *S. kurilensis* to near-negligible levels; the cover increased slowly after clear-cutting but remained below initial levels. Weeding or herbicide application resulted in different patterns with respect to height; height decreased rapidly in response to weeding, whereas herbicide application had more gradual effects. Height began to increase after clear-cutting, and *S. palmata* exceeded its initial height, reaching 1.5–2.0 m in the 10–15 years following clear-cutting. No tree recruits were found in sites where dwarf bamboo was left unmanaged. Weeding and herbicide application facilitated recruitment of *Betula ermanii* after clear-cutting, but recruits of *Fagus crenata*, which originally dominated the forest canopy, remained scarce or non-existent at 30 years after clear-cutting. We postulate that natural regeneration of *Fagus* is nearly impossible following clear-cutting in temperate beech forests in Japan with dense undergrowth of *Sasa*, even with advance measures to reduce or eliminate *Sasa*.

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*Fagus crenata*; long-term ecological research; Mt. Naeba Experimental Beech Forest; *Sasa kurilensis*; *Sasa palmata*

### Introduction

Dwarf bamboos are widely distributed from India to East Asia (Bystrakova et al. 2003; Kobayashi 2015). In Japan, dwarf bamboo species, one of the main components of natural plant communities, are distributed throughout the temperate region (Makita 1998). Although positive ecological roles have been postulated for dwarf bamboos (e.g. prevention of soil nutrient leaching, Watanabe et al. 2016; provision of wildlife habitat, Yamaura et al. 2008), their negative effects are much more pronounced. For example, dwarf bamboo is associated with decreased diversity of herbaceous species (Kobayashi et al. 1998; Kudo et al. 2011) and decreased growth of canopy trees (Takahashi et al. 2003; Ishii et al. 2008).

In the context of forest dynamics, disturbances such as logging or natural treefall promote the rapid spread of dwarf bamboos by creating a light environment optimal for their growth (Saitoh et al. 2000; Fukuzawa et al. 2015). This substantially inhibits post-disturbance tree recruitment and consequently reduces the sustainability of forest ecosystems (Akai 1972; Nakashizuka and Numata 1982a; Maeda 1988; Abe et al. 2001). In response to these challenges, bulldozers with grader blades have been used to remove dwarf bamboos, including underground rhizomes, at gently sloping sites (Umeki 2003). By contrast, in montane forests on steep terrain, which are common in Japan, such practices cannot be applied, and alternative approaches, including weeding and herbicide application, have been used to eliminate dwarf bamboo

(Kawahara 1978; Morisawa and Hoshino 2019). However, the long-term effects of these practices on both dwarf bamboo populations and tree regeneration have not been directly monitored and remain unclear.

In Japan, dwarf bamboo species with long, laterally spreading rhizomes (e.g. species of *Sasa*, *Pleioblastus*, and *Sasaella*, according to the nomenclature of Yonekura and Kajita (2003), which we use in the following text) are more common than those with short rhizomes and clumped culms (Konno 1977). Species with long rhizomes spread rapidly (Lieurance et al. 2018) and form large genets as long as several hundred meters (Suyama et al. 2000). Rhizomes often survive when aboveground organs are removed, subsequently producing new culms (Kawahara 1978; Morisawa et al. 2010); even when damaged, they may receive assimilation products from distant live culms in the same genet (Saitoh et al. 2000, 2002) that may promote their survival. Consequently, even when reduced by silvicultural practices such as weeding and herbicide application, long rhizomatous species are likely to return to their former abundance over time. It is thus critical to know for how long silvicultural treatments reduce aboveground dominance of dwarf bamboos; this in turn requires long-term investigation.

We monitored changes in the cover and height of two dwarf bamboo species of the genus *Sasa* in a temperate beech forest over a 41-year period, which included the 11-year period before clear-cutting and 30 years after clear-cutting. During the initial 11 years, weeding was performed or herbicide was applied repeatedly, partly accompanied by

soil scarification to facilitate seedling establishment. The occurrence and growth of tree recruits were also studied throughout the 40 years. Based on our analyses, we evaluated the effects of silvicultural treatments on the suppression of dwarf bamboo and the regeneration of two important canopy species, *Fagus crenata* and *Betula ermanii*, as impacted by competition with *Sasa* after clear-cutting. Finally, we discuss suitable management practices for sustainable forestry in temperate forests in Japan with dense understory dwarf bamboo.

## Materials and methods

### Study site

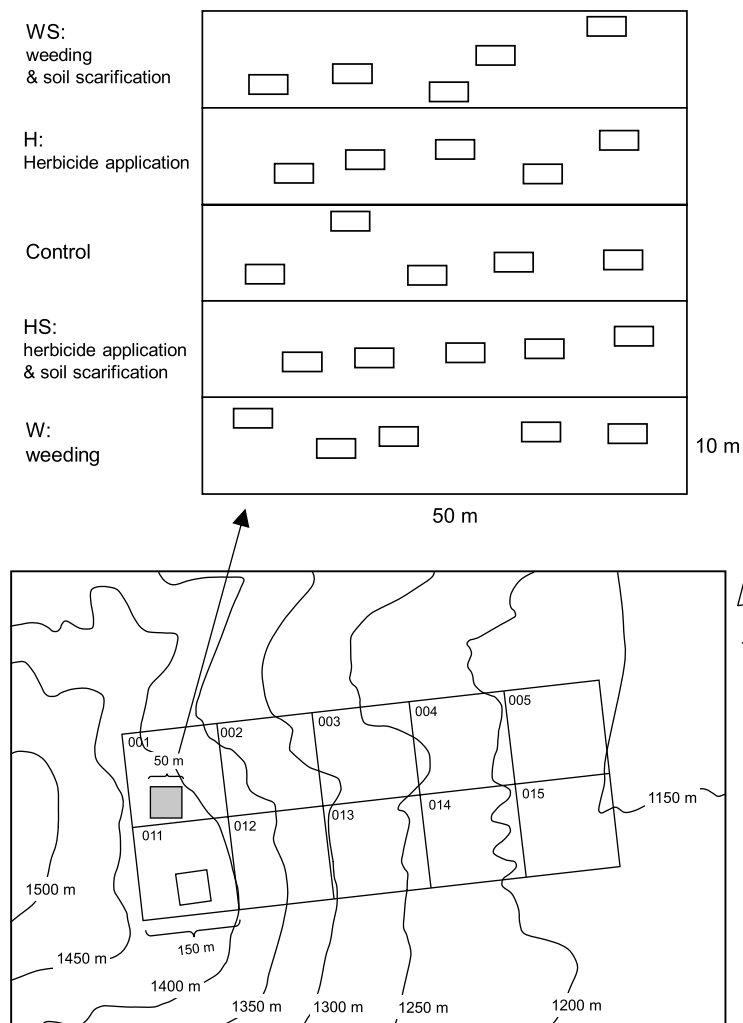
We collected field data in the Mt. Naeba Experimental Beech Forest, established in 1967 (Maeda 1988; Ogawa et al. 2005; Masaki et al. 2012). The site is located at 35.8864°–35.8883° N, 138.7300°–138.7389° E, at elevations of 1150–1450 m. Annual mean temperature is 5.4–6.3°C, annual precipitation is 2321–2391 mm, and the maximum snow depth in winter is 314–436 cm (Ogawa et al. 2005). Parent rocks include Andesite and volcanic ash, and slope angles are 17–28°.

A 300 × 750-m study area was established in this forest in 1967. This area was divided into 10 150 × 150-m plots

(Figure 1). These 10 plots were experimentally subjected to diverse cutting methods (clear-cutting, seed tree cutting, shelterwood cutting, selection cutting) or left uncut and the effects on the regeneration of *F. crenata* were examined (Maeda 1988). According to an inventory drawn up in 1993 for a 50 × 50-m subplot located within plot number 011, which was unlogged throughout the study period, the basal area was 34.1 m<sup>2</sup> ha<sup>-1</sup> and the canopy was composed of two species, *Fagus crenata* and *Betula ermanii*. The former made up the majority of the basal area (82%), whereas the latter accounted for a minor proportion (18%), which indicates that *F. crenata* was dominant in this forest in its original, old-growth state. Two dwarf bamboo species, *Sasa palmata* and *S. kurilensis*, formed dense understory vegetation (Maeda 1988; Ogawa et al. 2005), which is common in beech forests in regions of Japan that receive heavy snowfall (Hukusima et al. 1995). *F. crenata* had a mast year in 1976 and abundant seedlings of this species were observed in 1977 (Maeda 1988).

### Field methods

In the current study, we analyzed data collected from plot number 001, which was clear-cut in 1978. Logging was performed using chainsaws in the period from July to



**Figure 1.** Outline of the Mt. Naeba Experimental Beech Forest and the silvicultural treatments applied in the five blocks in the 50 × 50-m subplot (shaded square) established in plot 001. Five quadrats (2 × 4 m) were established at approximately 10-m intervals within each block for vegetation surveys. Plot 011 (open square) was not logged during the entire study period. An inventory was taken in 1993 within a subplot located in this plot.

August and fallen logs were collected in September using an overhead system of winch-driven cables (Dr. Wajiro Suzuki, personal communication).

A 50 × 50-m subplot was established within plot number 001 in 1967 (Figure 1). The subplot was divided into five blocks oriented perpendicular to slope contours, and different silvicultural treatments were applied in each block with the objective of decreasing or eliminating dwarf bamboos and promoting tree recruitment (Figure 1). The treatments included weeding (W), weeding with soil scarification (WS), herbicide application (H), herbicide application with soil scarification (HS), and no treatment (control). Careful and thorough manual weeding was conducted with sickles to a height of <20 cm. During the first weeding, trees of less than approximately 10 m tall were also cut within the weeded blocks, which was equivalent to salvage cutting. Cut stems, branches and leaves were piled at the boundaries of weeded blocks (Dr. Takeo Tanimoto and Dr. Wajiro Suzuki, personal communication). To apply herbicide, granules (50% sodium chlorate) were scattered at a density of 150 kg ha<sup>-1</sup> each time; this was the standard procedure for killing dwarf bamboo at that time (Toyooka and Shinozaki 1980). The soil was scarified by manual raking within one of the weeded blocks and one of the herbicide application blocks to turn over the fallen leaf layer and expose mineral soil; this process can be advantageous for the establishment of seedlings (e.g. Shibata et al. 2010).

The timing of the treatments listed above is summarized in Table 1 (see Maeda 1988; Ogawa et al. 2005). During the 11 years prior to clear-cutting in 1978, dwarf bamboo and other vegetation were weeded out three times in the W and WS treatments, herbicide was applied twice in the H and HS treatments, and soil was scarified twice in the WS and HS treatments. These treatments were applied in fall, with the exception of the herbicide application in 1972, which was conducted in early summer.

Five quadrats of 2 × 4 m were established within each block in 1968 to monitor vegetation and tree recruitment (Figure 1). Surveys were conducted annually between late summer and early fall from 1968 to 1982 and in 1986, 1992, 1997, and 2008. During each survey, the cover of each *Sasa* species was estimated using a modified Braun-Blanquet (BB) scale. Cover classes were V (75–100%), IV (50–75%), III (25–50%), II

(10–25%), I (<10%), and + (trace). The length of the tallest culm of each *Sasa* species in each quadrat was measured at the time of each survey. Stem lengths of tree recruits (seedlings and saplings) were also measured within each quadrat in each survey year. Because we used the data for the largest stem of each tree species and *Sasa* species in a quadrat, and the largest stems were mostly near vertical, we treated the lengths of the stems as heights. See Maeda (1988) and Ogawa et al. (2005) for further details regarding field methods.

### Statistical analyses

Although our objective was to evaluate the mean effects of each treatment on bamboo cover, categorical values cannot be averaged across quadrats; we, therefore, transformed the BB scale values into continuous variables. First, we determined the upper limit of the trace category, arbitrarily assuming that this category indicated that no more than a single leaf of a ramet was present per 1 m<sup>2</sup>. The leaves of both *Sasa* species measure approximately 5 × 30 cm. Assuming that leaves are elliptical in shape yields an area of 118 cm<sup>2</sup>, which implies that the upper limit of cover classified into the trace category is approximately 1%. Second, we developed five binary variables:  $B_V$ , which indicated that BB was either V or not V;  $B_{IV}$ , which indicated that BB was greater than or equal to IV;  $B_{III}$ , which indicated that BB was greater than or equal to III;  $B_{II}$ , which indicated that BB was greater than or equal to II; and  $B_I$ , which indicated that BB was greater than or equal to I. For example, BB III was represented by the combination of  $B_V = 0$ ,  $B_{IV} = 0$ ,  $B_{III} = 1$ ,  $B_{II} = 1$ ,  $B_I = 1$ . For the highest cover class (V) all values were 1, whereas for the lowest class (+) all values were 0. Finally, BB scale values were transformed using a hierarchical model within a Bayesian framework. If true cover was near the threshold between two classes, BB would be observed as belonging to either the upper or lower level with a probability of 0.5. Therefore, the probability that BB was greater than or equal to S (i.e.  $B_{S,i,y} = 1$ ) in quadrat  $i$  in year  $y$  can be expressed as

$$\text{logit}(P_{S,i,y}) = k_S(\text{logit}(C_{i,y}) - \text{logit}(R_S)) \quad (1)$$

where  $C_{i,y}$  and  $R_S$  represent the true cover values in quadrat  $i$  and year  $y$  and the lower threshold of the cover range corresponding to BB = S, respectively. The parameter  $k_S$  represents the slope of a logistic curve (Figure 2). Greater values of  $k_S$  represent smaller observation errors, and vice versa. Values of  $k_S$  were determined as follows:

$$B_{I,i,y} \sim \text{Bern}(P_{I,i,y}), \text{logit}(P_{I,i,y}) = k_I(\text{logit}(C_{i,y}) - \text{logit}(0.01)) \quad (2)$$

$$B_{II,i,y} \sim \text{Bern}(P_{II,i,y}), \text{logit}(P_{II,i,y}) = k_{II}(\text{logit}(C_{i,y}) - \text{logit}(0.1)) \quad (3)$$

$$B_{III,i,y} \sim \text{Bern}(P_{III,i,y}), \text{logit}(P_{III,i,y}) = k_{III}(\text{logit}(C_{i,y}) - \text{logit}(0.25)) \quad (4)$$

$$B_{IV,i,y} \sim \text{Bern}(P_{IV,i,y}), \text{logit}(P_{IV,i,y}) = k_{IV}(\text{logit}(C_{i,y}) - \text{logit}(0.5)) \quad (5)$$

**Table 1.** Timing of treatments in the subplots. Blocks are labeled as follows: W, weeding; WS, weeding + soil scarification; H, herbicide application; HS, herbicide application + soil scarification; Control, no manipulation. All treatments were applied in fall, except for the herbicide application in 1972 (applied in early summer). The entire plot, including the experimental blocks, was clear cut (CC) in 1978.

Year	Blocks				
	W	WS	H	HS	Control
1967			H	H	
1968	W	W, S		S	
1969		S		S	
1970					
1971	W	W			
1972			H*	H*	
1973	W	W			
1974					
1975					
1976					
1977					
1978	CC	CC	CC	CC	CC

\* Herbicide was applied in early summer

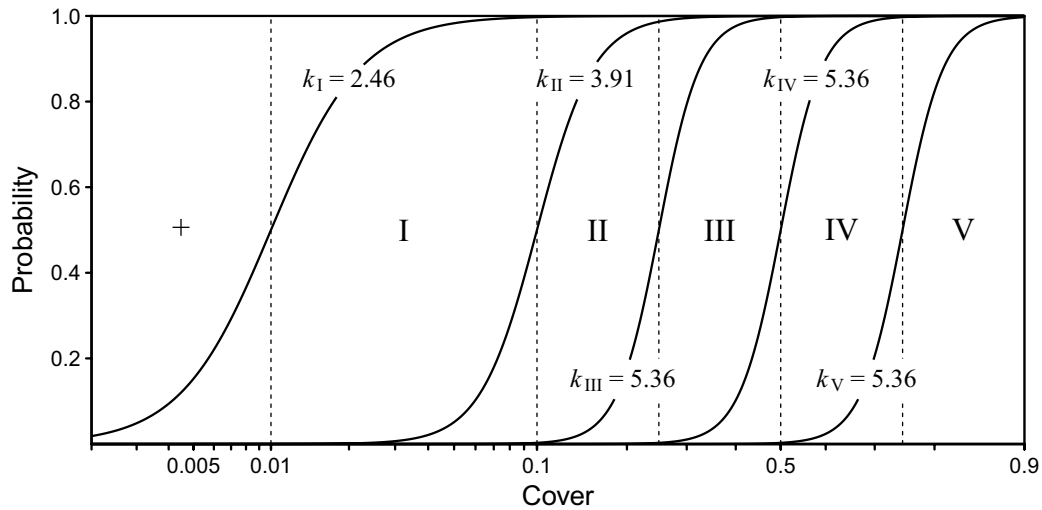


Figure 2. Logistic curves expressing detection accuracy for BB classes. Vertical dashed lines indicate class boundaries. Cover (0–1) is shown on a logit scale.

$$B_{V i,y} \sim \text{Bern}(P_{V i,y}), \text{logit}(P_{V i,y}) = k_V (\text{logit}(C_{i,y}) - \text{logit}(0.75)) \quad (6)$$

We assumed that  $\text{logit}(C_{i,y})$  followed a normal distribution with the logit of  $\mu_{C_{t,y}}$  as the mean and  $\sigma_{C_{t,y}}^2$  as the variance in year  $y$  and block  $t$  in which quadrat  $i$  was located. This relationship was described as follows:

$$\text{logit}(C_{i,y}) \sim N(\text{logit}(\mu_{C_{t,y}}), \sigma_{C_{t,y}}^2) \quad (7)$$

To avoid overparameterization of the model, we assumed that the variance  $\sigma_{C_{t,y}}^2$  was constant independent of block and year, and equation (7) is thus reconfigured as follows:

$$\text{logit}(C_{i,y}) \sim N(\text{logit}(\mu_{C_{t,y}}), \sigma_{C_{common}}^2) \quad (8)$$

The parameter  $\text{logit}(\mu_{C_{t,y}})$  was assumed to follow a normal distribution with hyperparameters, and the prior of parameter  $\sigma_{C_{common}}$  was assumed to be vague:

$$\text{logit}(\mu_{C_{t,y}}) \sim N(\text{logit}(\mu_{C_{hyper}}), \sigma_{C_{hyper}}^2) \quad (9)$$

$$\sigma_{C_{common}} \sim \Gamma(0.01, 0.01) \quad (10)$$

The priors of the hyperparameters were also assumed to be vague:

$$\text{logit}(\mu_{C_{hyper}}) \sim N(0, 0.01) \quad (11)$$

$$\sigma_{C_{hyper}} \sim \Gamma(0.01, 0.01) \quad (12)$$

The parameter  $\mu_{C_{t,y}}$  estimated in this model was the estimate of the mean cover of each *Sasa* species in block  $t$  and year  $y$ . We used the means and the 95% credible intervals of the posterior distributions as the representative values for each  $\mu_{C_{t,y}}$ .

We arbitrarily set values for  $k_I$ ,  $k_{II}$ ,  $k_{III}$ ,  $k_{IV}$ , and  $k_V$  according to the following procedures. We assumed that the detection error, both overestimates and underestimates, should be 0.05 at the midpoint of each BB class on a logit scale (Figure 2). For example, in a quadrat with a true cover value of 0.366 (the midpoint of BB = III on the logit scale), an observer might evaluate BB as either II with a probability of

( $P_{II} = 0.95$ ) or IV with the same probability ( $P_{IV} = 0.05$ ). Based on this assumption, we established  $k_I$  to yield a value of 0.95 for  $P_I$  at the midpoint of BB = I on the logit scale. The value of  $k_{II}$  was obtained as the mean of two values: one forcing a value of 0.05 for  $P_{II}$  at the midpoint of BB = I on the logit scale, and the other forcing a value of 0.95 for  $P_{II}$  at the midpoint of BB = II on the logit scale. Values of  $k_{III}$  and  $k_{IV}$  were calculated in the same way. The value of  $k_V$  was set such that the value of  $P_V$  was 0.05 at the midpoint of BB = IV on the logit scale. Using these procedures we derived the following values for  $k$ :  $k_I = 2.46$ ,  $k_{II} = 3.91$ ,  $k_{III} = 5.36$ ,  $k_{IV} = 5.36$ , and  $k_V = 5.36$  (Figure 2).

We estimated the mean height of the tallest *Sasa* culm for each block and year using similar procedures within this Bayesian framework. The logarithm of height in quadrat  $i$  in year  $y$ , or  $\log(H_{i,y})$ , was assumed to follow a normal distribution with the logarithm of the mean height in year  $y$  in block  $t$  in which quadrat  $i$  was located, with a mean of  $\log(\mu_{H_{t,y}})$  and a variance of  $\sigma_{H_{t,y}}^2$ :

$$\log(H_{i,y}) \sim N(\log(\mu_{H_{t,y}}), \sigma_{H_{t,y}}^2) \quad (13)$$

To avoid overparameterization, we assumed that variance was constant independent of block and year and that its prior was vague. Based on this we reconfigured equation (13) as follows:

$$\log(H_{i,y}) \sim N(\log(\mu_{H_{t,y}}), \sigma_{H_{common}}^2) \quad (14)$$

$$\sigma_{H_{common}} \sim \Gamma(0.01, 0.01) \quad (15)$$

The parameter  $\log(\mu_{H_{t,y}})$  was assumed to follow a normal distribution with hyperparameters, as follows:

$$\log(\mu_{H_{t,y}}) \sim N(\log(\mu_{H_{hyper}}), \sigma_{H_{hyper}}^2) \quad (16)$$

The hyperparameters were also assumed to have vague priors, as follows:

$$\log(\mu_{H_{hyper}}) \sim N(0, 0.01) \quad (17)$$

$$\sigma_{H_{hyper}} \sim \Gamma(0.01, 0.01) \quad (18)$$

Using the estimates of  $\log(\mu_{Ht,y})$  and  $\sigma_{Hcommon}^2$ , which are the parameters of a lognormal distribution, the mean of the distribution,  $E_{Ht,y}$ , was derived using the equation:

$$E_{Ht,y} = \exp(\log(\mu_{Ht,y}) + \sigma_{Hcommon}^2/2) \quad (19)$$

The derived  $E_{Ht,y}$  provided an estimate of the mean height of the tallest *Sasa* culm in block  $t$  in year  $y$ . We used the mean and 95% credible intervals of the posterior as the representative values for each  $E_{Ht,y}$ .

We performed the above analyses for both *S. kurilensis* and *S. palmata*. For *S. kurilensis*, some records indicated a BB class of + and a height of 0 cm. Because complete disappearance from a quadrat was unlikely (see Results), we assumed that this indicated the presence of plants <1 cm tall, which was the minimum unit of the rulers used in the field. To analyse height data on a log scale, we assigned 0.5 cm to these cases (i.e. the midpoint between 0 and 1 cm).

The occurrence and growth of *F. crenata* and *B. ermanii* recruits were analyzed as follows: We used the maximum height of each species in each quadrat in the analyses, because other representative values such as the mean and median heights were found to be highly sensitive to annual variation in the abundance of small seedlings and were therefore not reliable indicators of regeneration. Furthermore, we excluded quadrats with no recruits, rather than including these quadrats and assigning heights of 0 cm to non-existent seedlings. Thus, the values estimated here represented the mean maximum heights of trees that actually occurred in the quadrats. Thereafter, the mean maximum heights of tree recruits across quadrats, in each block in each year, were estimated in the same way as *Sasa* and

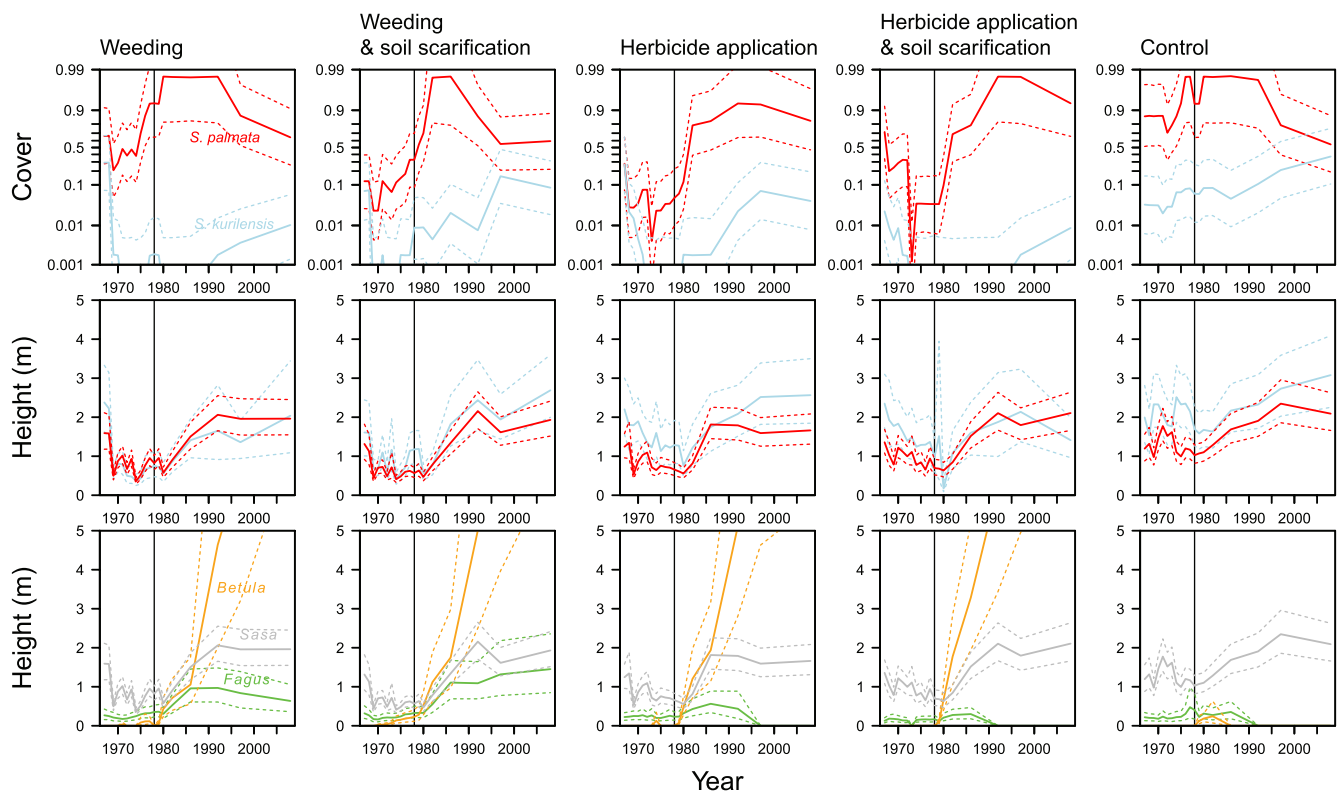
compared to the heights of *Sasa* ( $E_{Ht,y}$ ). When visualizing temporal changes in height in graphs we recorded tree height as 0 cm when no tree recruits occurred in any quadrat within a given block and year.

We estimated parameter distributions using JAGS in R version 3.6.1 (R Core Team 2019) with the package rjags (version 4.3.0) (Plummer 2003). The number of chains was set to three. The number of steps for each chain was 22,000 and was thinned by 20 steps after the removal of the first 2000 steps, resulting in 1000 samples from the posterior for each chain. Gelman and Rubin's convergence diagnostic ( $\hat{R}$ ) (Gelman and Rubin 1992) never exceeded 1.02, and all chains appeared to converge well.

## Results

### Cover of dwarf bamboo

Estimated temporal changes in cover (0–1) of *Sasa* are shown in Figure 3. *S. palmata* showed large variation in cover among blocks, with values ranging from 0.1 to 0.9 throughout the study period. In the control block, cover remained constant at >0.9 before and shortly after clear-cutting but began to decrease 15 years after clear-cutting, reaching approximately 0.5 at the end of the study period. In the W treatment, weeding rapidly lowered cover from 0.5 to 0.2, but cover began to increase prior to clear-cutting and soon reached nearly 0.99; trends thereafter were similar to the control block. Cover in the WS treatment was initially lower than in the W treatment and remained lower immediately after treatment but subsequently showed a similar pattern to the W treatment. In the H treatment, cover decreased substantially to <0.01 after treatment but began



**Figure 3.** Estimated changes in mean cover (upper panels) and height (middle panels) of *Sasa palmata* (red) and *S. kurilensis* (light blue) over time in each treatment. Solid vertical lines represent the year of clear-cutting. Changes in the mean maximum heights of *Fagus crenata* (green) and *Betula ermanii* (orange) recruits within each block are shown with those of *Sasa* (lower panels). In the lower panels, the plots of *Sasa* heights were constructed from measurements taken on the more abundant of the two congeners (in this case, they are identical to height of *S. palmata* because it always had greater cover values than *S. kurilensis*). Dashed lines represent 95% credible intervals. The cover of *Sasa* (0–1) is shown on a logit scale (vertical axes of an upper panel).

increasing after the last herbicide application prior to clear-cutting, reaching more than 0.9 about 15 years after clear-cutting and decreasing gradually thereafter. Trends in response to the HS treatment were very similar to those for the H treatment.

Cover of *S. kurilensis* was initially lower than the cover of *S. palmata* in all blocks. All treatments reduced the cover of *S. kurilensis* to very low levels (<0.001), but this species began to recover after clear-cutting, albeit at a slower rate than *S. palmata*. In particular, cover remained almost negligible for 15–25 years after clear-cutting in the W and HS treatments. In the control treatment, cover increased gradually after clear-cutting and reached 0.4, the highest value observed in any treatment.

### Height of dwarf bamboo

Temporal changes in the height of *Sasa* are shown in Figure 3. *S. palmata* was 1.0–1.5 m tall at the beginning of the study. In the control treatment, height remained unchanged prior to clear-cutting and increased gradually thereafter, reaching approximately 2.0 m after 20 years. In the W and WS treatments, height decreased abruptly to 0.5–1.0 m immediately after the treatments. In the H and HS treatments, height decreased gradually to 0.5 m. After clear-cutting, height began to increase rapidly and reached 1.5–2.0 m in 10–15 years in treated blocks.

The height of *S. kurilensis* was 1.5–2.0 m at the beginning of the study. In the control block, heights remained essentially unchanged prior to clear-cutting but increased gradually after clear-cutting, reaching approximately 2.5 m at the end of the study period. Almost the same patterns as *S. palmata* were found before clear-cutting in treated blocks. Heights increased gradually after clear-cutting and reached 0.6–2.0 m, with lower values found in the W blocks and higher values found in the WS blocks.

### Height of tree recruits

Temporal changes in the maximum height of tree recruits are shown in Figure 3. Seedlings of *F. crenata* were observed in all blocks prior to clear-cutting. After clear-cutting, seedlings persisted in the W and WS treatments, but their average maximum height never exceeded that of *S. palmata* in the 30 years following clear-cutting. In the H, HS, and control treatments, *F. crenata* seedlings disappeared within 20 years of clear-cutting.

Seedlings of *B. ermanii* appeared after application of the W and WS treatments and grew rapidly after clear-cutting, reaching heights of 3 m within 10 years and far overtopping co-occurring *Sasa* plants, and finally reaching 17–20 m after 30 years (Figure 4). In the H and HS treatments, seedlings appeared immediately after clear-cutting and grew rapidly, as in the W and WS treatments, reaching >10 m in height after 30 years. Seedlings were observed in the control treatment shortly after clear-cutting but soon disappeared.

We observed variation in regeneration patterns among quadrats within the same treatment (Figure 5, Table 2). In the last year of our study (2008), recruits of *F. crenata* were present in 60% and 80% of the quadrats in the W and WS treatments, respectively, but recruits that grew taller than *Sasa* were found in only 20% and 40% of the quadrats assigned to these treatments, respectively. Tree heights

reached <4 m, and the average density of trees higher than *Sasa* was no more than one tree per quadrat. In contrast, recruits of *B. ermanii* were present and grew taller than *Sasa* in 60% of the quadrats in the W and WS treatments, and in 80% of the quadrats in the H and HS treatments. The density of *B. ermanii* taller than *Sasa* reached 2–6 trees per quadrat on average.

Other woody species taller than *Sasa* were found in 2008, but they were less frequent and shorter in height than *Betula* (Table 2). These were typically subcanopy species in the W and WS treatments with densities of <2 per quadrat and reaching <8 m in height (occasionally ca. 10 m for *Chengiopanax sciadophylloides*) and shrub species mainly in the H treatment with densities of <1 per quadrat and reaching <5 m in height. There were few subcanopy and shrub species in the HS and control treatments.

## Discussion

### Effects of treatments on dwarf bamboo

In spite of a 10-year pre-treatment period prior to clear-cutting, no treatment was effective at eliminating local *Sasa* populations. Treatments such as weeding and herbicide application initially decreased the cover of *S. palmata* to less than 20%, but these plants recovered their original cover values and increased their dominance after clear-cutting. Although all treatments decreased the height of *Sasa* plants by a minimum of 0.5 m, both species recovered or exceeded their original height within 5–10 years of clear-cutting. These results agree with previous findings that imply that dwarf bamboos benefit from increased light availability after clear-cutting (Fukuzawa et al. 2015). Cover of *S. kurilensis* decreased more drastically and was slower to recover (>10 years) compared to *S. palmata*, but *S. kurilensis* never completely disappeared and often exceeded its original height after clear-cutting. Overall, *S. palmata* always had a greater average cover than *S. kurilensis*, suggesting that *S. palmata* had a more significant influence on tree regeneration at the study site.

Our findings show that suppressing *Sasa* is quite challenging, even with repeated treatments during a 10-year period under a closed beech canopy. A likely mechanism underlying the tolerance of *Sasa* species to treatments is their rhizomatous growth form (Saitoh et al. 2000); the rhizomes likely form a connection between damaged *Sasa* in the treatment blocks and undamaged *Sasa* in the control block or outside of the subplots. Rhizomatous *Sasa* plants often form large genets that extend to distances of more than 100 m (Suyama et al. 2000), and assimilation products are transferred between ramets, serving to maintain the cover and growth of ramets in shaded environments (Saitoh et al. 2002). Quadrats treated with weeding or herbicide application were within 10 m of untreated areas. Thus, plants damaged by the treatments likely received assimilation products from ramets outside the blocks, facilitating their recovery. Furthermore, it is likely that quadrats were colonized by *Sasa* ramets growing adjacent to study plots via rapid rhizome expansion (Kudo et al. 2011; Lieurance et al. 2018). This process likely promoted the prompt recovery of *Sasa* plants both prior to and after clear-cutting.

For *S. palmata*, the transfer of assimilation products via the rhizomes might explain the different effects of weeding



**Figure 4.** A photograph taken of the W treatment area in 2014 showing dense *Sasa palmata* undergrowth. A 180-cm tall individual wearing a white hard hat can be seen standing in the image among several stems of *Betula ermanii*. An unlogged stand (plot 011) can be seen in the background.

and herbicide application. First, in the herbicide treatments, it took longer for *S. palmata* to reach cover values >90%, and maximum cover values remained lower than in the weeded blocks even though herbicide was applied less frequently than weeding procedures. This might be because herbicide causes greater damage to rhizomes than weeding. In general, weeding removes the aboveground parts of plants but does not directly damage underground parts. In contrast, sodium chlorate, the herbicide used in this study, generally impacts all organs (Manabe 1969). Second, the timing of the onset of recovery is worth noting. In the weeding treatments, *S. palmata* cover began to increase prior to clear-cutting, whereas recovery began after clear-cutting in the herbicide treatments, suggesting that rhizomes with less damage might promote earlier recovery. Third, weeding and herbicide application had different effects on the height growth patterns of *Sasa*; at least in this study, weeding decreased the height of both species immediately, whereas herbicide application resulted in gradual decreases in height, implying cumulative effects over time. As stated above, weeding did not directly damage the rhizomes, and weeded plants likely photosynthesized in newly formed leaves (using resources from rhizomes) in the window of high light conditions just before leaf out in the forest canopy in spring and after leaf fall from the forest canopy in autumn (Lei and Koike 1998). By contrast, damage to rhizomes in the herbicide treatments

impeded surviving *S. palmata* from growing until clear-cutting substantially increased the light availability.

Although herbicide caused greater reduction of *Sasa* than weeding, it did not permanently eliminate *Sasa*. Other studies have reported that the effects of herbicide do not persist over the long term at sites characterized by thick soils with abundant organic matter (but its mechanisms were not clarified) (Toyooka and Shinozaki 1980). The B<sub>D</sub> soil type (Forest Soil Division 1976) found at our study site (Maeda 1988; Ogawa et al. 2005) may have also limited the duration of herbicide effects. In addition, it is possible that herbicide leached from the soil at our study site, which was located on a slope and received abundant precipitation (>2300 mm year<sup>-1</sup>).

The timing of treatments may also explain their limited effects. Weeding, and one of the herbicide applications, was implemented in fall. It is recommended that weeding be conducted in August in Japan (Kawahara 1978), when energy reserves in rhizomes are at their minimum (Suzuki and Stuefer 1999). Herbicides are also most effective when applied in August because metabolic activity is higher and consequently absorption is higher than at other times of the year (Miyake 1962). Conducting silvicultural treatments in summer rather than autumn might more effectively suppress the growth of *Sasa*.

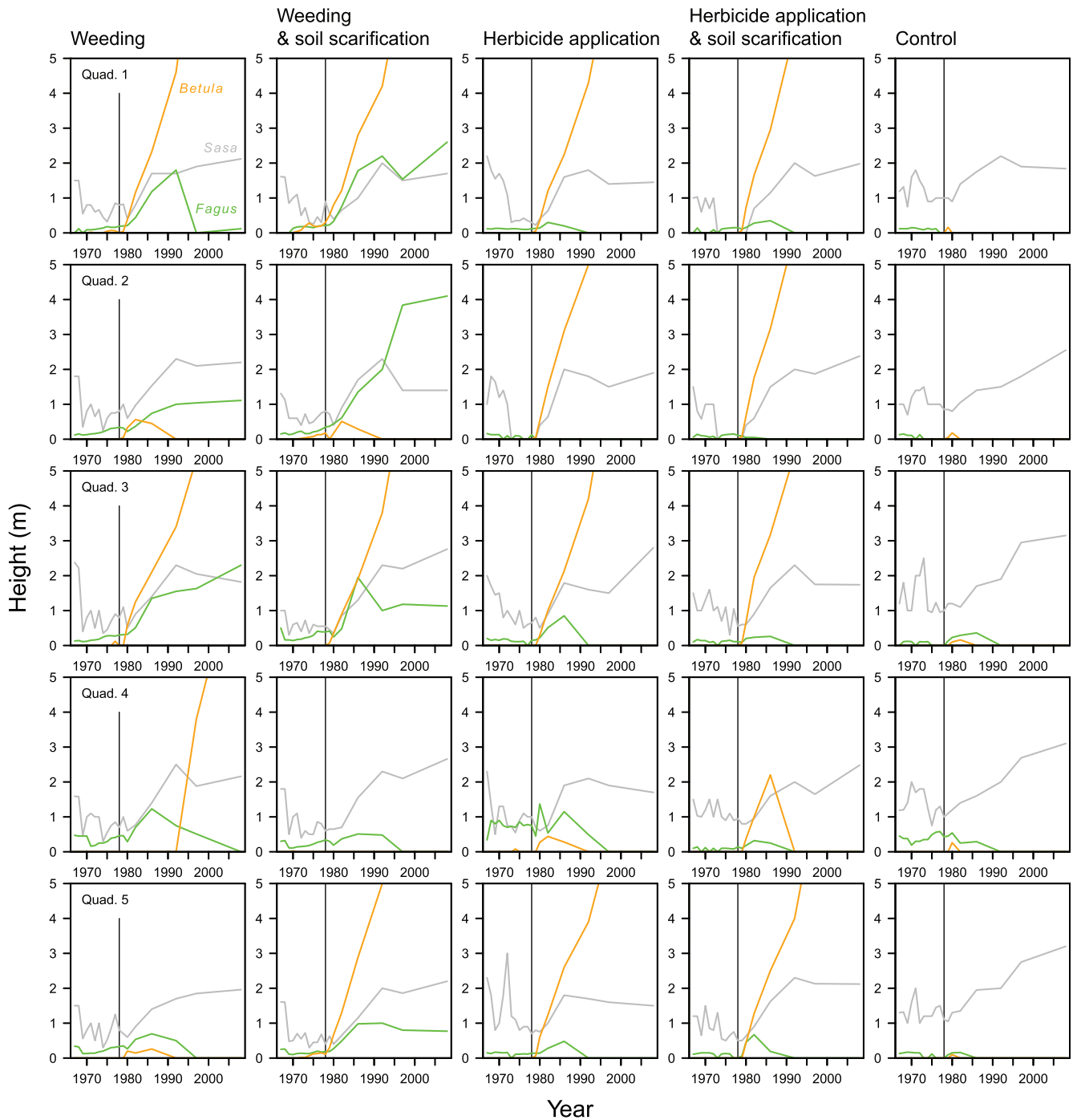
There were differences in treatment effects between *S. palmata* and *S. kurilensis*. *S. palmata* began to recover before or immediately after clear-cutting in all treatments, whereas *S. kurilensis* was often slower to recover. Furthermore, decrease in cover and height associated with treatments were more conspicuous in *S. kurilensis*, although this species is generally taller than *S. palmata* (Konno 1977). It is unlikely that this difference between species resulted simply from interspecific competition, because *S. kurilensis* increased its cover under competitive pressure from *S. palmata* in the control block. *S. kurilensis* has fewer buds on its culms and rhizomes, and smaller biomass stores in its rhizomes than *S. palmata* (cf. Konno 1977). We speculate that *S. kurilensis* may thus be more vulnerable to external disturbances and take longer to recover.

### Effects of dwarf bamboo on tree regeneration

No recruits of canopy tree species were observed in the control block, even 30 years after clear-cutting; however, tree seedlings were present in other treatments. This confirms previous findings that the absence of *Sasa* facilitates tree regeneration in beech forests (e.g. Nakashizuka and Numata 1982b; Abe et al. 2002). In general, only 2% of sunlight reaches the ground surface in stands with dense *Sasa* populations, even in open habitats; this impedes the growth and survival of tree seedlings (Akai 1972). We have provided additional evidence that dense *Sasa* cover substantially inhibits tree regeneration after canopy disturbance.

Tree recruitments occurred in blocks other than the control block, but the composition differed substantially from the original canopy. Prior to clear-cutting, the canopy was dominated by *F. crenata* (>80% of the basal area), but following treatment, recruits of *B. ermanii* overtopped the *Sasa* layer more often than recruits of *F. crenata*. *Fagus crenata* seedlings only survived in the weeded blocks after clear-cutting, but on average their growth was stagnant and they were largely suppressed by *Sasa* even 30 years after clear-cutting.





**Figure 5.** Changes in the maximum height of *Sasa* (gray), and recruits of *Fagus crenata* (green) and *Betula ermanii* (orange) in each quadrat in each block. The plots of *Sasa* height were constructed from measurements taken from the more abundant of the two congeners (i.e. greater cover value) in each year.

*F. crenata* had mast seeding in 1976 at the study site, and many seedlings remained at the time of clear cutting in 1978 (Maeda 1988). Nevertheless, clear-cutting promoted the spread of dwarf bamboo throughout the study site, precluding regeneration of *F. crenata*. This is an important lesson for the management of *F. crenata* forests.

In natural beech forests in Japan with dense *Sasa* undergrowth, regeneration of beech is considered possible only in infrequent microsites with low dwarf bamboo density (Tanaka 1988; Nakashizuka 1989). Similarly, we found that when *Sasa* bamboos were weeded out, a few *F. crenata* grew faster than recovering *Sasa* in 20–40% of the quadrats, likely forming small foci of regeneration. From a long-term perspective, such patchy regeneration might be adequate at a stand level for reforestation toward the original condition, i.e., dominated by *F. crenata*.

However, the weeding in this study was performed much more carefully and thoroughly than is the case in actual forestry practice; the cost was not considered in the experimental practice. This implies that sustainable management of *F. crenata* populations via clear-cutting is almost impossible at sites with dense *Sasa* cover, even with advanced treatment to reduce *Sasa* abundance. We should therefore refrain from clear-cutting *F. crenata* forests with dense *Sasa* populations.

It is worth noting that *F. crenata* seedlings did not establish in the herbicide treatments. Sodium chlorate damages not only *Sasa* but also woody species (Kataoka and Miyahara 1962; Manabe 1975). However, seedlings of *B. ermanii* grew steadily in the same blocks. Therefore, it is unlikely that herbicide application was the only factor that prevented the establishment of *F. crenata* seedlings. Another possibility is

**Table 2.** Tree and shrub species that were taller than dwarf bamboo in 2008 for each treatment. A pair of numerical values is shown for each species in each treatment: average density per quadrat (left) and occurrence frequency (%) within the five quadrats in the treatment (right). Horizontal bars represent absences.

Species	W		WS		H		HS		Control	
Canopy species										
<i>Betula ermanii</i>	1.4	60%	2.4	60%	2.2	80%	5.8	80%	–	–
<i>Fagus crenata</i>	0.4	20%	1.0	40%	–	–	–	–	–	–
Subcanopy species										
<i>Cornus controversa</i>	1.8	60%	0.6	20%	–	–	–	–	–	–
<i>Fraxinus lanuginosa</i>	0.2	20%	–	–	–	–	1.8	20%	–	–
<i>Chengiopanax sciadophylloides</i>	0.4	20%	0.4	20%	–	–	–	–	0.4	40%
<i>Sorbus commixta</i>	–	–	1.2	60%	–	–	–	–	–	–
<i>Padus grayana</i>	–	–	0.8	40%	0.2	20%	–	–	–	–
<i>Acer rufinerve</i>	0.2	20%	0.2	20%	–	–	–	–	–	–
<i>Acer nipponicum</i>	–	–	–	–	–	–	–	–	0.2	20%
Shrub species										
<i>Viburnum furcatum</i>	–	–	0.4	40%	0.8	80%	0.4	40%	0.4	40%
<i>Acer australe</i>	–	–	0.6	60%	0.4	40%	–	–	–	–
<i>Lindera umbellata</i> var. <i>membranacea</i>	0.2	20%	–	–	0.4	40%	–	–	–	–
<i>Magnolia salicifolia</i>	–	–	–	–	0.2	20%	–	–	–	–

that the sodium chlorate prevented the germination of *F. crenata* seeds, but this also seems unlikely considering that such an effect would require extremely high amounts of sodium chlorate (Asanuma et al. 1984). Instead, the cause may have been an indirect effect of herbicide application; recruitment of other woody plants, such as shrubs, may have been facilitated by the decreased *Sasa* coverage after clear-cutting, and the slower-growing *F. crenata* seedlings might have been suppressed by shrubs. Although shrubs in 2008 were often found within a block where herbicide was applied, these ideas remain speculative and need to be explored in greater detail. At present, we can conclude that herbicide application is not effective at promoting regeneration of *F. crenata* after clear-cutting at sites with dense *Sasa* cover.

### Future directions

In this study, during the first 20–30 years after clear-cutting, the cover of *S. palmata* increased and then returned to initial values in both treatment and control blocks. It is unclear whether this was due to suppression by regenerating *B. ermanii* or to reactive processes internal to *S. palmata*. Longer-term monitoring at the study site, along with *in-situ* physiological studies of *Sasa*, is necessary to further explore this pattern.

If this decreasing trend continues, growth of surviving suppressed *F. crenata* seedlings in weeded blocks may accelerate, and these populations may eventually overtop *Sasa* plants. However, it is unlikely that *F. crenata* will recolonize the herbicide and control blocks even in the event of decreased *Sasa* cover, because the probability of seeds being dispersed from distant conspecific adults is low (Masaki et al. 2019); rather, other shade-tolerant species with greater dispersal capacities may colonize instead (e.g. *Acer*; Masaki et al. 2019). Even if *Betula* species colonize after clear-cutting, decrease in *F. crenata* populations have negative ecological consequences, because adult trees of the latter species support diverse wildlife; for example, they provide food for vertebrates in the form of seeds (e.g. Oka et al. 2004) and nesting cavities and roosting sites for birds (e.g. Ogasawara and Izumi 1978). Thus, colonization of *F. crenata*, including the provision of wildlife habitat, is critical from an ecosystem management perspective. We should therefore monitor tree recruitment in the herbicide and control blocks to evaluate the potential for restoring critical ecosystem functions.

At forest sites on gentle slopes, historic livestock grazing and the harvesting of understory biomass by locals likely prevented the dominance of dwarf bamboo (>50 years ago) in Japan (e.g. Aoki and Nakamura 2002; Sugita et al. 2006). Under such circumstances, *F. crenata* accumulates sapling banks under the forest canopy and regenerates steadily after clear or partial cutting of the forest (Maeda 1988). Currently, some landowners remove *Sasa* rhizomes using machinery such as backhoes or bulldozers with grader blades (Umeki 2003); however, it is physically impossible to do this in forest stands on steep slopes or in remote regions. The results of this study imply that unless effective and enduring *Sasa* control practices can be developed, clear-cutting of natural forests with dense *Sasa* undergrowth, which is common in Japanese temperate forests (Hukusima et al. 1995; Makita 1998), should be avoided for sustainable forest ecosystem management.

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






### Disclosure statement

We have no potential conflict of interest.

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## Geolocation information

The study site location: 36. 8872° N, 138.7308° E

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