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Distribution and synchronized massive flowering of *Sasa borealis* in the forests of Korean National Parks

Soyeon Cho, Youngjin Kim and Yeonsook Choung*

Abstract

Background: Genus *Sasa*, dwarf bamboos, are considered to be species that lower biodiversity in the temperate forests of East Asia. Although they have a long interval, they, the monocarpic species, have a unique characteristic of large-scale synchronized flowering. Therefore, once they have flowered and then declined, it may be an opportunity for suppressed surrounding species. A previous study reported that *Sasa borealis* showed specialized flowering nationwide with a peak in 2015. However, this was based on data from a social network service and field survey at Mt. Jeombong. Therefore, we investigated *S. borealis* in the forests of five national parks in order to determine whether this rare synchronized flowering occurred nationwide, as well as its spatial distribution.

Results: We found a total of 436 patches under the closed canopy of *Quercus mongolica*-dominated deciduous forests in the surveyed transects from the five national parks. Of these patches, 75% occupied a whole slope area, resulting in an enormous area. The patch area tended to be larger in the southern parks. Half (219 patches) of the patches flowered massively. Among them, 76% bloomed in 2015, which was consistent with the results of the previous report. The flowering rate varied from park to park with that of Mt. Seorak being the highest. The culms of the flowering patches were significantly taller (F = 93.640, $p < 0.000$) and thicker (F = 61.172, $p < 0.000$). Following the event, the culms of the flowering patches declined, providing a good opportunity for the suppressed plant species. The concurrent massive flowering of the mature patches was believed to be triggered by some stress such as a spring drought.

Conclusion: We confirmed that the rare synchronized flowering of *S. borealis* occurred with a peak in 2015 nationwide. In addition, we explored that *S. borealis* not only monopolized an enormous area, but also dominated the floors of the late-successional *Q. mongolica*-dominated deciduous forests. This presents a major problem for Korean forests. As it declined simultaneously after flowering, there are both possibilities of forest regeneration or resettlement of *S. borealis* by massively produced seeds.

Keywords: Dieback, Forest dynamics, Mass flowering, Semelparous reproduction, Simultaneous flowering

Background

Qian and Ricklefs (1999, 2000) stated that the Eastern Asian phytogeographic zone, which includes the Korean peninsula, belongs to one of the highest diversity groups within the world's temperate forests. For example, the forest flora of the Korean Peninsula is more diverse than that of comparable forests in Europe and North America (Qian and Ricklefs 2000).

However, the Genus *Sasa*, dwarf bamboos, is widespread and dominant in the lower strata of the East Asian forests. They have been known to be species that inhibit species diversity and tree regeneration (e.g., Nakashizuka and Numata 1982; Ito and Hino 2007; Cerny et al. 2013, 2015). Cho et al. (2018) reported that plant species diversity was significantly reduced with the dominance of *Sasa borealis* in the forests of Gangwon Province, Korea. Due to the clonal growth habit, it forms a dense mono-stand that physically occupies the aboveground and underground spaces and lowers the light intensity reaching the floor (Wada 1993; Park et al. 2012).

* Correspondence: yschoung@kangwon.ac.kr
Department of Biological Sciences, Kangwon National University, Chuncheon 24341, South Korea

Moreover, it has a long life span (Makita 1998) and slow decomposition rate (Narukawa and Yamamoto 2002). Although it is a native species, it exhibits characteristics similar to invasive species.

Clonal plants, such as *Sasa* species, rapidly expand horizontally without a suitable pollinator. With their high morphological plasticity, they adapt well to environmental stress (Harper 1977). Moreover, their high shade tolerance makes them capable of invading stable mature forests in China. For example, Moso bamboo (*Fargesia decurvata*), a dwarf bamboo, has invaded a fir forest (Liu et al. 2011), mixed forests (Shen et al. 2016), and evergreen broad-leaved forests (Yang et al. 2011). Even dominant species have been changed (Hong et al. 2004). In addition, the shoot can grow fast, reaching its maximum height within 70 days, with support from the underground rhizome.

Sasa borealis is a native species that is very widespread throughout Korea (Lee and Lim 2002). Cerny et al. (2013, 2015) studied forest vegetation, including national parks in Korea, and stressed that the dominance of *S. borealis* is the most important factor hindering the succession of the Korean forests. Further, it is possible that *S. borealis* is controlled naturally. Many bamboo species have distinctive flowering characteristics. After about 10 to 100 years of vegetative growth, most of the genets flower simultaneously and decline (Janzen 1976; Taylor and Zisheng 1988; Makita 1992). Although it is not easy to observe the flowering events because of the long intermast intervals, synchronized flowering and dieback of the *Sasa* species have also been reported (e.g., Makita 1998). The simultaneous decline following the flowering of *S. borealis* contributed to the regeneration of the suppressed plants (Nakashizuka 1988).

Recently, Cho et al. (2017) reported that nationwide synchronized flowering of *S. borealis* occurred at its peak in 2015 in Korea. This study was meaningful insofar as being the first study revealing the rare flowering event of *S. borealis* in South Korea. Aside from a direct field survey of Mt. Jeombong, most information was based on the social network service recorded by mountain visitors. Because national parks are popular places, it is possible that several observers will record the flowering phenomenon in the same place.

Nationwide massive flowering of *S. borealis* is very rare. If it withers within a short time after the flowering, it could then be a significant influence on the dynamics of the forest occupied by the species. Therefore, we investigated the flowering and decline events of *S. borealis* along with the spatial distribution in the forests of five national parks.
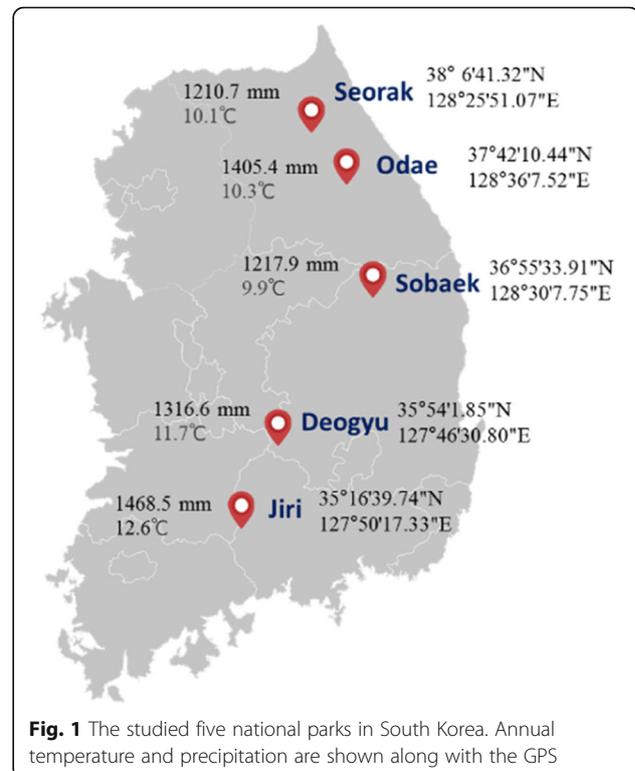
Methods

Studied national parks and investigated transects

Most national parks in South Korea are located along the great mountain range, Baekdudaegan, from north to south. Among the national parks, Mts. Seorak, Odae, Sobaek, Deogyu, and Jiri were selected (Fig. 1) and surveyed in the summer of 2017. A total of 25 transects (trails) were set considering the park area and distribution of *S. borealis* (Table 1). In total, 133.5 km from the transects was surveyed. The distance of each transect varied according to its topography. The topography of Mt. Seorak was more complicated than that of the other mountains. The northern part was steep, while the southern part, where Mt. Jeombong is located, was gentle. Therefore, we surveyed the longest distance of 34.9 km in Mt. Seorak National Park. Mts. Odae, Sobaek, and Deogyu were each explored by four transects. Mt. Jiri, the largest park area, was explored by five transects with a distance of 31.2 km. The annual precipitation and temperature were high with more rainfall in the southern parks, reflecting the effects of the latitude (Fig. 1; Korea Meteorological Agency 2017).

Vegetation survey and data analysis

We investigated all transects from the trail starting point at low regions climbing toward the higher ones, such as ridges or tops. In each transect, all of the patches of *S. borealis* on both sides of the trails were surveyed. A patch was defined as an area where *S. borealis* grew densely and could be visually distinguished from the surrounding area. Each patch size was divided into four classes: ≤ 100 m^2, $100 \sim 1000$ m^2, $1000 \sim 2500$ m^2, and whole slope. The

Fig. 1 The studied five national parks in South Korea. Annual temperature and precipitation are shown along with the GPS

Table 1 Investigated transects and the distances in five national parks

National park (area)	Transect	Distance (km)
Seorak (398 km^2)	Seorakdong Park Information Center-Sinheungsa-Biseondae	3.0
	Hangyeryeong Resting Place-Hangyeryeongsamgeori-Gwittegicheongbong	2.8
	Osaek Ranger Station-Seonnyeotang-Geumgangmun-Yongsopokpo	3.2
	Seorakdong Park Information Center-Yukdampokpo-Biryongpokpo-Towangseongpokpo Observation	2.8
	Pilryeyaksu-Mangdaeamsan (Mt. Jeombong)	0.9
	Gangseon Village-Gombaeryeong (Mt. Jeombong)	8.1
	Ganeungol-Danmokryeong (Mt. Jeombong)	7.0
	Garimakgol-Saeyanggol (Mt. Jeombong)	7.1
Odae (326 km^2)	Sangwonsa-Horyeongbong	1.7
	Sangwonsa-Woljeongsa	8.1
	Jingogae-Dongdaesan-Dongpigol	4.4
	Sinsungol	0.9
Sobaek (322 km^2)	Eouigok Park Information Center-Birobong	4.8
	Eouigok Park Information Center-Sangwuelbong	4.5
	Jungnyeong Park Information Center-Yeonhwabong-Huibangpokpo	9.5
	Jungnyeong Resting Place-Dosolbong	5.9
Deogyu (229 km^2)	Gucheondong Park Information Center-Hyangjeokbong	7.0
	Yeonggak Park Ranger Post-Namdeogyusan-Wolseong Park Ranger Post	8.4
	Gucheondong Park Information Center-Sindae Resting Place-Baengnyeonsa-Hyangjukbong	7.8
	Hwangjeom Park Ranger Post-Satgatbong	4.4
Jiri (483 km^2)	Seonggamjae Ranger Station-Nogodan	2.1
	Eumjeong-Yeonhacheon Shelter-Hyeongjebong-Byeoksoryeong Shelter	12.1
	Jungsanri Visitor Center-Cheonwangbong	5.4
	Yeongwonsa-Sambulsa	6.3
	Jungsanri Visitor Center-Jeseokbong	5.3
Total		133.5

'whole slope' referred to cases where one patch covered the entire slope, or the patch continued to cover other slopes, making it difficult to estimate the area.

For each patch, the presence of inflorescences was examined then classified into "flowering" and "non-flowering" patches. The flowering time of a flowering patch was identified empirically according to the state of the inflorescence. Inflorescences flowered in 2017 (referred to as "2017F") had a vivid purple flower at the time of the survey. Those that flowered in 2016 (2016F) remained only as florets without fruits, and most of their leaves withered. Those flowered in 2015 (2015F) showed signs of inflorescence, but all of the florets were gone and their leaves were completely dried. Some of the patches showed signs of flowering before 2015. Even though we assumed that this had happened in either 2013 or 2014, it was difficult to exactly specify the time of occurrence. In that case, we assigned it to "pre-2015F." The "non-flowering" patches indicate those with no signs of flowering. When only a few culms had

inflorescences within a patch, it was designated as a non-flowering patch. Within each patch, a 50 × 50 cm plot was set up. Culms were identified as alive, declined, or flowered, then tallied respectively. The shoot heights and basal diameters of the five culms were measured.

The differences in culm density and size in accordance with the flowering state were analyzed by a randomized block design analysis of variance (ver. 23, SPSS 2016). The national park was assigned as a block source. The effects of density, thickness, and height on flowering absence or presence, respectively, were analyzed. For the flowering, 2015F, 2016F, and 2017F were pooled, and pre-2015F was excluded from the analysis. The early-flowered culms were likely to be relatively drier; thus, the height or diameter of the culms may be underestimated.

In each forest, the locations of patches were divided into four layers: tree (≥ 8 m in height), subtree (5 ~ 8 m), shrub (1 ~ 5 m), and herb layers. The coverage of each layer was estimated visually, and the vegetation type was

identified. The elevation and slope were measured, and the topography was recorded.

For spring precipitation, those from Inje, Hongcheon, Bonghwa, and Geochang Counties were used for Mts. Seorak, Odae, Sobaek, and Deogyu, respectively (Korea Meteorological Agency 2017). For Mt. Jiri, the mean value of Sancheong and Namwon was used.

Results

Distribution of *S. borealis*
In total, 436 *S. borealis* patches were found from five national parks, with 44.5% distributed in Mt. Seorak. Among all patches, 75% were large enough to cover the entire slope. They were found at elevations ranging from 188 to 1618 m. This indicates that this species could grow from low to high tops (Table 2). The patches were also found on gentle to steep slope areas, even though it showed poor growth in steeper slope areas. They were more common in lower slope areas and near valleys. This trend held for all five national parks.

S. borealis occurred at the forest floor of the closed canopy mainly dominated by *Quercus mongolica* and mixed with other late-successional deciduous trees, such as *Acer*, *Tilia*, *Carpinus*, and *Fraxinus*. In some stands, especially on Mt. Jiri, *Q. mongolica* exclusively

dominated. On the other hand, *Abies holophylla* was dominant and mixed with deciduous trees above, including *Q. mongolica* on Mt. Odae. This also occurred in the *Larix leptolepis* plantations for a few patches on Mt. Sobaek.

Synchronized massive flowering of *S. borealis*
We found 50% flowered patches out of the total 436 patches (Fig. 2). Among the five national parks, Mt. Seorak had the highest flowering rate of 74%. The flowering rates of Mts. Odae and Jiri were 49% and 37%, respectively. By contrast, those of Mts. Sobaek and Deogyu were 3% and 18%, respectively. In 2015, 76% of flowering patches were bloomed (Fig. 3). Specifically, it happened in all five national parks, unlike in the other years. Additionally, more patches bloomed in 2015, with the exception of Mt. Deogyu. In 2017, there were 13 and 10 flowering patches in the southern parks of Mt. Jiri and Mt., respectively.

Within patches, over 90% of the culms bloomed at pre-2015F to 2016F patches, and the rate was lower in 2017F patches (Fig. 4). In the three mountains of Mts. Seorak, Jiri, and Deogyu, some culms (0.9%) flowered from the non-flowering patches. This phenomenon was found to be more common along paths with sunlight.

Table 2 Distribution of *S. borealis*, site characteristics, and vegetation layer structure of the surveyed plots from the five national parks

Properties		Seorak	Odae	Sobaek	Deogyu	Jiri
S. borealis patches	No. of patches found	202	41	32	71	90
	Patch size (m^2)					
	Whole slope (%)	67[1]	85	91	94	67
	1000 ~ 2500 (%)	8	0	0	0	2
	100 ~ 1000 (%)	16	5	3	3	7
	≤ 100 (%)	9	10	6	3	24
Vegetation	Type	*Quercus mongolica*-dominated deciduous forest	*Abies holophylla* mixed deciduous forest	*Quercus mongolica*-dominated deciduous forest	*Quercus mongolica*-dominated deciduous forest	*Quercus mongolica*-dominated deciduous forest
	Layer structure					
	Tree layer (%)	91.7 ± 0.4	90.4 ± 1.0	89.6 ± 1.3	90.1 ± 1.2	85.2 ± 1.4
	Subtree layer (%)	32.9 ± 1.3	40.8 ± 3.2	36.1 ± 3.2	47.2 ± 2.8	58.4 ± 2.3
	Shrub layer (%)	29.6 ± 1.3	26.1 ± 2.0	27.2 ± 2.2	33.1 ± 2.1	32.6 ± 1.3
	Herb layer (%)	65.2 ± 2.6	86.7 ± 2.8	90.8 ± 2.0	94.3 ± 1.0	91.6 ± 0.5
Site	Elevation (range, m)	188–1097	672–1172	741–1317	634–1610	630–1618
	Slope (range, °)	5–50	5–35	10–60	5–60	0–70
	Topography					
	Valley and lower slope (%)	72[2]	73	50	39	48
	Upper and middle slope (%)	16	27	38	34	33
	Ridge and top (%)	13	–	13	27	19

(1) Relative frequency of each patch size within a park. In Mt. Seorak, frequency was calculated except for eight missing patches
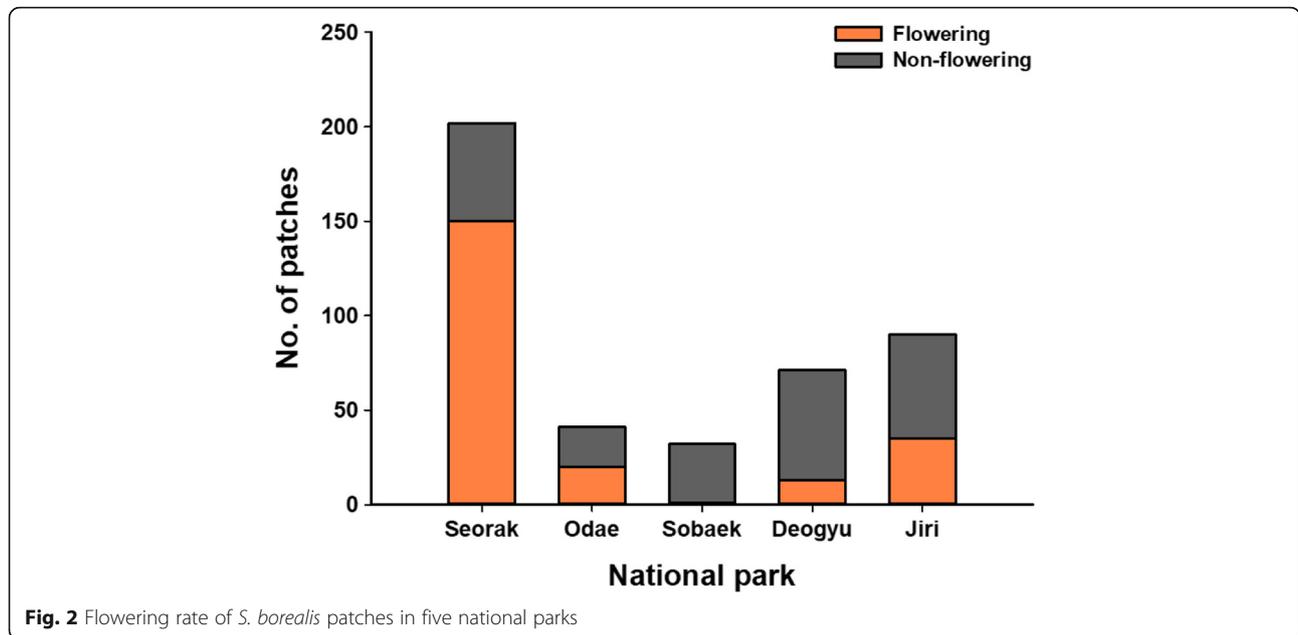(2) Relative frequency of each topography within a park

Fig. 2 Flowering rate of *S. borealis* patches in five national parks

The densities, heights, and diameters of culms were significantly different among the national parks (Table 3). The culm densities of the northern mountains of Mts. Seorak and Odae were higher. By contrast, those of the southern mountains of Mts. Jiri and Deogyu were lower. The size was larger for the latter two mountains. The culm density was shown to be lower at the flowering patches. However, they were not significantly different from the non-flowering patches (F = 0.675, p = 0.412, Fig. 5). On the other hand, the culm height and thickness were significantly taller (F = 93.640, p < 0.000) and thicker (F = 61.172, p < 0.000) at the flowering patches. This indicates that larger culms flowered.

The spring precipitation from February to May was considered to be one of the potential factors influencing the flowering, according to Cho et al. (2017) (Fig. 6). 2015, the most flowered year, experienced a drought in springtime. In particular, those of Mts. Seorak and Odae were only 61% and 62% of the average precipitation for 30 years, respectively. Moreover, in 2014, the spring rainfall was only 53% and 41%, resulting in a cumulative drought consecutively. Unlike the two mountains in the north, those of Mts. Deogyu and Jiri were 91% and 95%, respectively, and did not suffer drought. Therefore, the high flowering rates of the two mountains in the north in 2014 and 2015 may have been related to the spring drought. In the
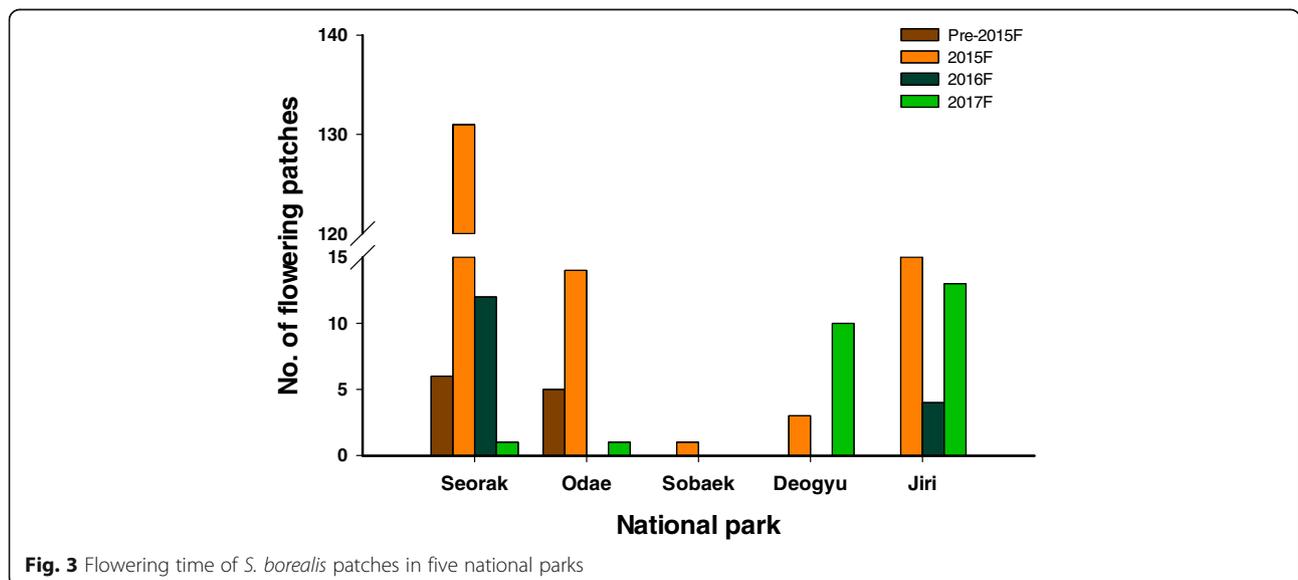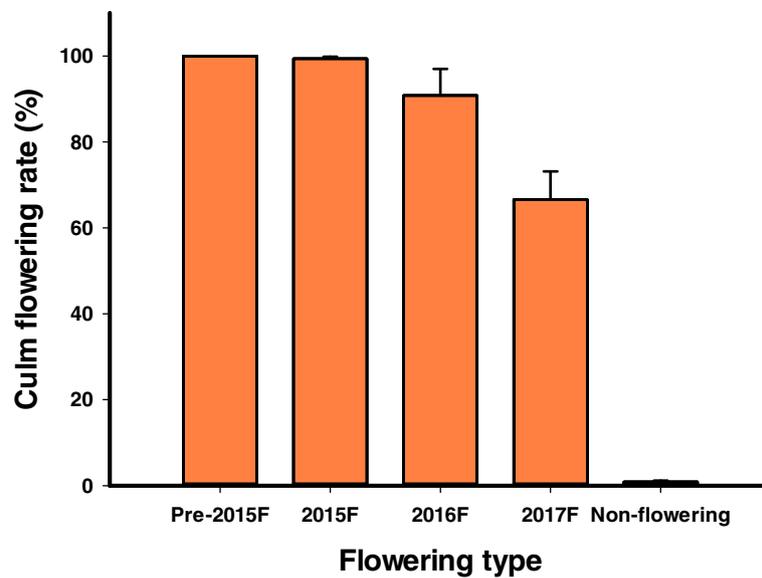

Fig. 3 Flowering time of *S. borealis* patches in five national parks

Fig. 4 Culm flowering rate in five national parks. Values are means ± standard errors

spring of 2017, there was a spring drought again and more patches flowered in the southern two parks.

Synchronized dieback following the flowering events of *S. borealis*

Over 99% of the culms in the pre-2015F and 2015F patches declined after flowering. We observed that the culms were declining immediately after flowering and completely died in Mt. Jeombong within 1 year (Cho et al. 2017). Compared to this, that of the culms in the 2016F patches was lower at 80.7%. 15.6% of culms had also declined in the non-flowering patches (Fig. 7).

Discussion

We found 436 patches of *S. borealis* in the investigated transects of the five national parks. The distribution area and dominance were more important than the patch number in that it occupied enormous slope area. Of the

Table 3 Analysis of variance for culm density, height and diameter according to the flowering status by randomized block design

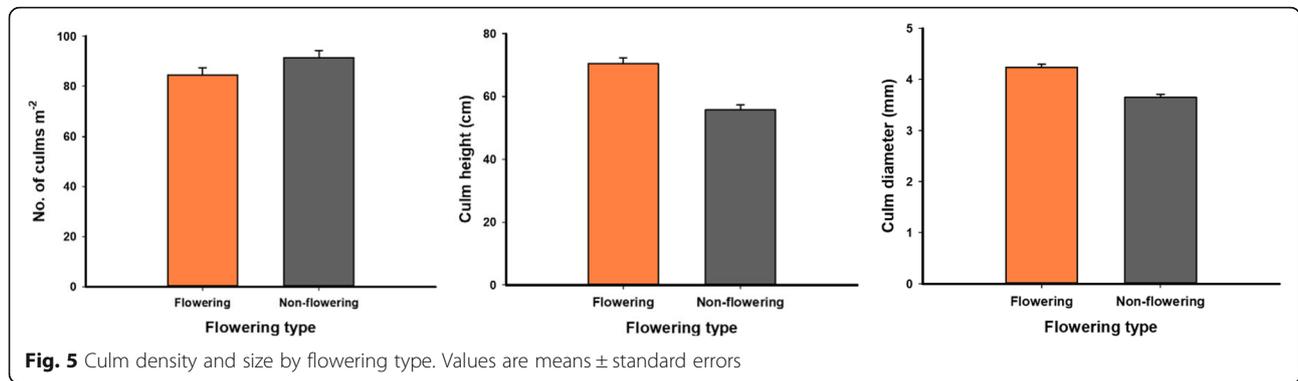| Source	df	F value	p value
Culm density			
National park	4	5.781	0.000
Flowering type	1	0.675	0.412
Culm height			
National park	4	22.685	0.000
Flowering type	1	93.640	0.000
Culm diameter			
National park	4	12.751	0.000
Flowering type	1	61.172	0.000

S. borealis patches we found, 75% were huge, as they tended to cover the entire slope. Most of the patches were estimated to be several tens of ha. In one transect going up to the highest peak of Mt. Jiri, a patch covered a path from an elevation of 800 m to 1600 m, about 2.5 km long. Similar cases were also observed in Mts. Deogyu (from 600 to 1400 m, 2.4 km long) and Sobaek (from 870 to 1100 m, 1.4 km long).

Consistent with the results of Cho et al. (2018), it was distributed mainly in the late-successional forests where *Q. mongolica* dominated. In fact, *S. borealis* flourishes as if there are virtually no limitations. There is little information on how this species expands and flourishes. It could be presumed that this is because of its reduced use. Instead, Yamamoto et al. (1995) reported that *Sasa* spread was related to large-scale natural disturbances, such as landslides. Until the 1970s, large-scale disturbances in forests, including slash-and-burning, intensive forest use, and frequent forest fires, were presumed to be the leading causes of expansion. However, it is also possible that it could expand in a stable forest as well. According to two permanent plot studies, the frequency and abundance of *S. borealis* have increased in Mts. Gyebang (Cheon et al. 2014) and Odae (Choung et al. unpublished) over the prior 10 years.

Half of all *S. borealis* patches were found to have flowered within a few years of this study. Specifically, 76% of the flowering patches bloomed in 2015, consistent with the findings from the SNS information and some observations (Cho et al. 2017). The massive flowering of *Sasa* plants has been extensively studied and reviewed in Japan (Makita 1998). This is because in Japan, there are more kinds of bamboo than Korea, and the distribution

Fig. 5 Culm density and size by flowering type. Values are means ± standard errors

area is wide. Oshima (1961) stated that it covered approximately 50% of the national parks in Japan and accounted for over 90% of the distribution in Hokkaido. Moreover, the flowering scale has been reported to range from several tens to 20,000 ha (Makita 1998). Its occupation in Korean national parks may be comparable, even though we have not been able to measure the scale.

The five national parks we explored are geographically separated. Nevertheless, there was a phenomenon of synchronized flowering. What caused this rare unique event? The answer to this is unclear, and there have been several hypotheses regarding it, such as a biological clock (Janzen 1976), cytokine control (Nadgauda et al. 1990), environmental stresses such as drought (Lowrie 1900), and/or a combination of these (Franklin 2004). Cho et al. (2017) supported the stress hypothesis that the drought may have triggered the flowering of *S. borealis*, similar to this study. In fact, the droughts in the spring of 2014 and 2015 were severe in the northern region (Mun and Lee 2015; Park et al. 2015). At that time,

most of the patches in Mt. Seorak were flowered. The values were very high compared to that of Mt. Jiri. Another drought event occurred in 2017. More patches flowered in Mts. Jiri and Deogyu in that year than in Mt. Seorak. Despite the drought in 2017, the reduced flowering in Mt. Seorak may have been because most of the patches (74%) had flowered before that year, resulting in not many non-flowering patches remaining.

Park and Choi (2017) claimed that the flowering of *S. borealis* may be triggered by a specific gene that is periodically expressed in a biological clock, regardless of external environmental factors. This is because spring drought has occurred frequently in the past. Additionally, in Japan, *S. borealis* flowered in a large scale in 2016. In addition, flowering has been synchronized in recent years, with a peak being experienced in 2015. *S. borealis* would have settled more than several hundred years at least, although we do not know how long it had maintained on this land. If so, the population in Korea may be a complex of patches of different

Fig. 6 Springtime precipitation between February and May in five national parks
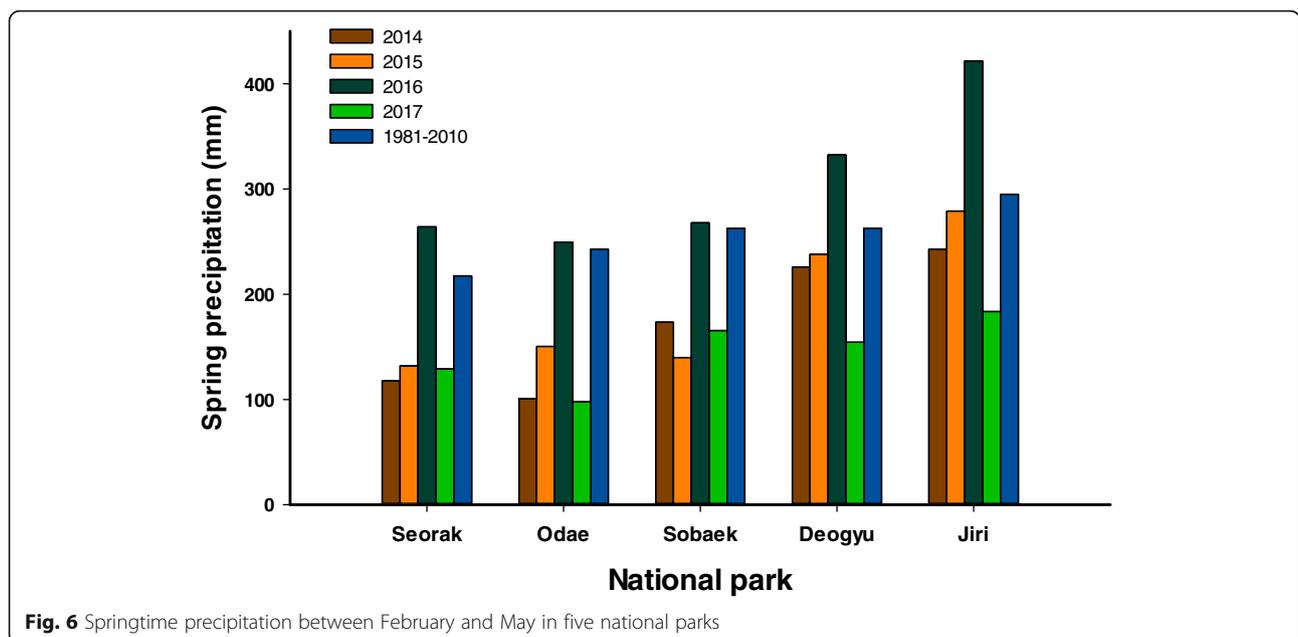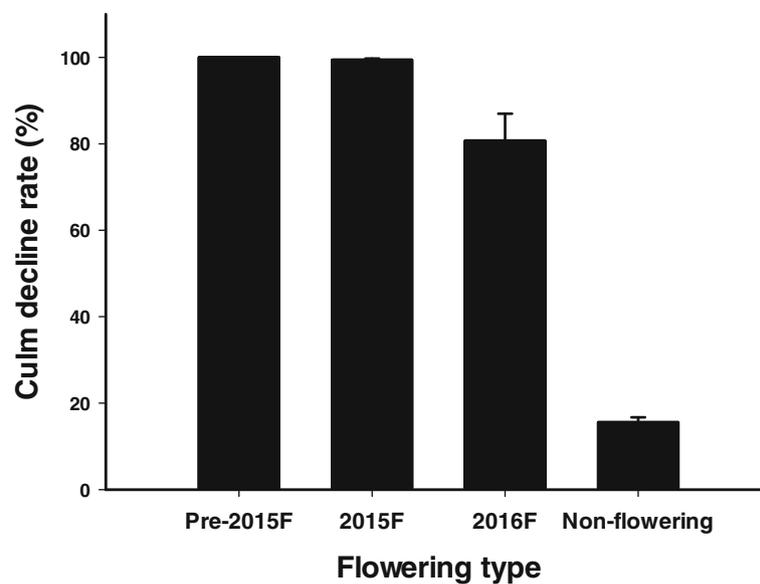
Fig. 7 Culm decline rate after flowering in five national parks. Values are means ± standard errors

biological ages. Therefore, it is difficult to make the assumption that the flowering was controlled by the same biological clock for the patches of different ages in the separated national parks. We found that patches with larger culms that were sufficiently mature were reproduced. Taken together, it is more reasonable to assume that flowering and drought are related. The specific mechanism of flowering requires further research.

A few culms, 0.9%, also flowered at the non-flowering patches, commonly along sunny trails. This could reflect sporadic flowering of a minority of culms in the culm population (Yamazaki and Nakagoshi 2005; Abe and Shibata 2014). *S. veitchii* var. *hirsute* showed sporadic flowering before and after mass flowering (Abe and Shibata 2012). It could be caused by the fact that one patch has been composed of multiple genets so that it had more than one flowering schedule, like the *Bambusa arnhemica* (Kaneko et al. 2008).

The flowering of *Sasa* species was considered to be important for the regeneration of forest (Nakashizuka 1988; Abe et al. 2001). This is because other suppressed species by *Sasa* could be regenerated if they declined after flowering (Taylor and Zisheng 1988; Makita 1992). The decline of *S. borealis* could have effects, such as creating gaps in forests. This could be an opportunity for buried seeds and/or for the advanced regeneration of the surrounding vegetation. Qian et al. (2016) stated that due to dense culms, the incoming seeds were effectively hidden, thus positively affecting the seed retention of the tree species. In regards to that, the seed stored in the soil had a chance to regenerate quickly following the decline. Moreover, the decline of *S. kurilensis* led to an increase in the survival of

Acanthopanax sciadophylloides, *Fagus crenata*, *F. lanuginosa*, *Kalopanax pictus*, and *Sorbus commixta*, as well as the emergence of *Acer japonicum*, *F. crenata*, *Fraxinus lanuginosa*, and *Tilia japonica* (Abe et al. 2002).

In order to expect these effects, the dieback of the flowered culms should be assumed soon after flowering. *Sasa quelpartensis*, distributed in Jeju Island, had massive flowering of 770 m^2 in 2017 (Northeastern Asia Biodiversity Institute 2017). However, it did not decline, so the effects of horse grazing and cutting are currently being investigated. However, in this study, *S. borealis* declined by 99% of culms in the 2015F and Pre-2015F patches, while the culms in the 2016F and 2017F patches showed lower rates. This may be due to the process of declining or small-sized patches under 100 m^2 being particularly slow, especially in Mt. Jiri.

Conclusion

We found that rare synchronized flowering of *S. borealis* occurred with a peak in 2015 nationwide. In addition, we determined that it not only monopolizes an enormous area, but also dominates the floor of the late-successional *Q. mongolica*-dominated deciduous forests. This is a major problem in Korean forests in that it has a tremendous impact on forest structures. The simultaneous decline following flowering could be an opportunity for forest regeneration, which means the natural control of this problematic species, *S. borealis*. On the other hand, it may resettle by the massively produced seeds. Therefore, the long-term monitoring on the forest dynamics is needed.

Availability of data and materials
The datasets during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Authors' contributions
SC, YK, and YC designed and carried out field experiments. SC analyzed the data and wrote the manuscript. YC reviewed and edited the manuscript. All the authors approved the manuscript.

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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