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短 報（Note）

Flowering culm dynamics in sporadic flowering of *Sasa cernua* Makino

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Abstract

Dwarf bamboo species are monocarpic, flower simultaneously, and die at intervals of several decades. The type of flowering ranges from sporadic to gregarious. We investigated sporadic flowering in *Sasa cernua*, one of the major dwarf bamboo species in central Hokkaido, by mapping all culms and studying their flowering status. An important finding of this study is that a single culm flowers twice over two consecutive years. In the major flowering year, some culms were significantly larger than the rest and showed evidence of preceding flowering. This indicated that at maturity size is one requirement for the flowering potential of *S. cernua.* All individual culms that have flowered once died after the major flowering year. Secondary flowering was observed in July of major flowering year in small study plot where seed fertilization did not take place. We also observed that new shoots with inflorescence alone were emerged in the following year to the major flowering. The unit size of the flowering patch of *S. cernua* was assumed to be 250 to 1000m^2 in the study area.

Key words : dwarf bamboo, monocarpic, *Sasa*, simultaneous flowering, sporadic flowering

Introduction

Dwarf bamboos are distributed widely in temperate and subarctic forests in Japan, often dominating the forest floor and preventing seedling establishment and successful regeneration of other plants. They are monocarpic and take several decades to flower. The simultaneous flowering and subsequent death of dwarf bamboos has a crucial impact on forest dynamics (Yamamoto *et al*., 1995; Nakashizuka, 1988). These impacts include altered light and soil conditions of the forest floor where seedlings of various plant species are expected to establish (Kudoh & Ujiie, 1990; Yamazaki & Nakagoshi, 2005; Abe *et al*., 2005) and provide a large number of viable seeds for insects (Kudoh *et al*., 1994; Nishiwaki & Makita, 1998) and mammals (Abe *et al*., 2001) as a nutrition. Therefore, knowledge of regeneration process is critical to understand the long-term forest dynamics in terms of the flowering behavior of dwarf bamboos on the forest floor.

The magnitude of simultaneous flowering and subsequent death for monocarpic dwarf bamboo varies from the large-scale gregarious flowering (Makita, 1992; Makita *et al*., 1988) to the small-scale sporadic flowering (Kudoh *et al*., 1994; Yamazaki & Nakagoshi, 2005). The flowering interval of the long-lived monocarpic bamboo (*Phyllostachys pubescens*) has been determined to be 67 years by observing the whole life cycle twice (Watanabe *et al*., 1982; Nagao & Ishikawa, 1998). Isagi *et al*. (2004) reported that the synchronous flowering of *P. pubescens* is genetically regulated. However, we do not yet know the factors regulating simultaneous flowering process of dwarf bamboo species, such as the age of flowering, or what regulates the flowering range.

Regionally synchronized large-scale gregarious flowering and death of dwarf bamboos is prominent and captures the attention of scientists (e. g. Makita, 1992). In contrast, small-scale sporadic flowering rarely merits detailed study. However, sporadic flowering can be considered the minimum unit size of a flowering patch, and possibly a good indicator for genet size if flowering were genetically controlled for dwarf bamboo species. Yet, individual identification using genetic markers is necessary to conclude whether a flowering unit is a genet or not. It is also important to obtain detailed information on the spatial distribution of flowering culms and flowering dynamics.

In the broadleaf forest in Sapporo, central Hokkaido, we observed sporadic flowering of *Sasa cernua*, one of the major dwarf bamboo species. *Sasa cernua* is known to be monocarpic (Kudoh & Ujiie, 1990; Janzen, 1976), although the flowering phenomenon is not yet fully understood. We took advantage of this opportunity to investigate the distribution of flowering culms in sporadic flowering patches of *S. cernua* in order to understand small-scale flowering dynamics of dwarf bamboo species.

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Materials and Methods

Study species

The genus *Sasa* is known to have 35 species distributed in Japan, Sakhalin, the Kuriles, and Korea (Suzuki, 1978). *Sasa* section Macrochlamys Nakai is distributed mainly in northern Japan.

The study species, *S. cernua*, has been confused with *S. kurilensis* in central Hokkaido. The species at this study site has sometimes been identified as *S. kurilensis* (e. g. Morita, 1975). We took this opportunity to identify this species using spikelet characters. The study species was identified as *S. cernua* Makino because it has minute hairs on culm-sheaths and leaf-sheaths, and 13 veins on the lower glume (Mikio Kobayashi pers. com.) whereas, the vegetative organ of *S. kurilensis* are glabrescent (Suzuki, 1978). *S. cernua* is of putative hybrid origin (Usui, 1961) between section Macrochlamys and section Sasa.

Study site

We observed a couple of sporadic flowering patches of *S. cernua* from 2003 to 2006 in the experimental forest of Hokkaido Research Center, Forestry and Forest Products Research Institute, Sapporo, Hokkaido (42°58' 32'' N, 141°23' 46'' E, 130 −260 m above sea level). *Sasa cernua* flowers in mid-May and produces seeds in July in this forest. This is a secondary forest with various broadleaf tree species, such as *Betula platyphylla*, *B. maximowicziana*, *Acer pitum* (*A. mono*), *A. japonicum*, *Quercus crispula*, *Magnolia hypoleuca* (*M. obovata*), and *Kalopanax pictus*. The maximum snow depth is approximately 75cm. Two dwarf bamboo species, *S. cernua*, and *S. senanensis* [(Franch. & Savat.) Rehd.] co-occur at this site (Hokkaido Branch, Forestry and Forest Products Research Institute, 1983). These two dwarf bamboo species are mixed and densely cover the forest floor of the study site. A somewhat gradual shift of abundance is observed; however, according to altitude, the proportion of *S. cernua* increases in over approximately 200m of elevation.

We established three study plots for sporadic flowering of *S. cernua* in the experimental forest (Plots 1, 2, and 3). Plot 1 was a flowering patch, contiguous to *S. senanensis* vegetation with a few culms of *S. senanensis* established within the boundaries. In Plot 2, *S. cernua* was sparsely distributed and co-occured with *S. senanensis*; however, the majority of *S. senanensis* had flowered and subsequently died. The forest floor is completely covered with dense *S. cernua* in Plot 3. Plot 1 flowered over an area of approximately 625 m^2 in May 2004 (Fig. 1a). Plots 2 and 3 flowered in May 2006 over areas of approximately 250 m^2 and 1600 m^2, respectively (Fig. 2a and b). For Plots 1 and 2, all culms were in the flowering patch, while for Plot 3 only a 10 m x 50 m patch in the middle of the flowering area was selected for study due to the large size of the flowering patch. The locations of all living culms within the plots, and the status of each culm—flowering or vegetative—were recorded. The size of each culm was determined to be the longest length of the living shoot regardless of the main shoot or substituted shoots. The major flowering year was the year in which the highest number of flowering culm within each study site was observed; 2004 for Plot 1, and 2006 for Plots 2 and 3. We also surveyed preceding flowering culms by identifying the remains of dead inflorescences in the main flowering year. We also observed secondary flowering when new flowering shoots or inflorescences were observed after May of the main flowering year. In addition, we checked the survival of flowering culms in Plot 1 in June 2005

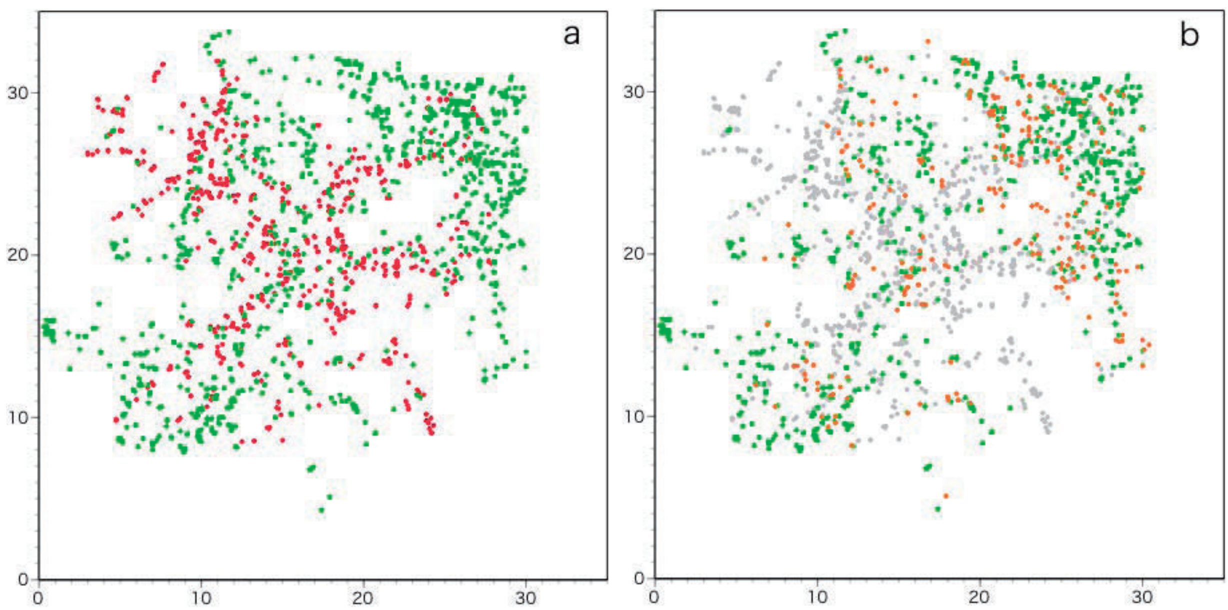

Fig. 1. Culm positions in Plot1 in 2004 (a) and 2005 (b). Scales are given in meters. Red circle, flowering culm; green, vegetative culm; grey, dead culm; yellow, new culm

Table 1. Three study plots for sporadic flowering of *S. cernua*

	Plot1		Plot2		Plot3	
Major flowering year	2004		2006		2006	
Average culm length (cm)	114.8		124.8		125.4	
Flowering patch area (m^2)	625.0		250.0		1600.0	
Surveyed area (m^2)	625.0		250.0		500.0	
Total number of culms	1715		415		2529	
Culm density (culms/m^2)	2.74		1.66		5.05	
	flowering	vegetative	flowering	vegetative	flowering	vegetative
Average culm length (cm)	132.2	104.0	128.2	119.3	126.6	123.7
Number of culms	657	1058	259	156	1529	1000
Proportion (%)	38.3	61.7	62.4	37.6	60.5	39.5
Density (culms/m^2)	1.05	1.69	1.04	0.62	3.06	2.0

and Plots 2 and 3 in June 2007.

Significant *t*-test was carried out for differences in culm size between status (flowering or vegetative).

Results

Flowering culms were found in the proportion of 38.3%, 62.4%, and 60.5% in Plots 1, 2, and 3, respectively (Table 1). The average length of flowering culms in the major flowering year was significantly larger than vegetative culms in Plots 1 and 2 (p<0.01), but not significant in Plot 3. Seeds were produced in July in Plots 1 and 3, but not in Plot 2.

We did not observe secondary flowering in Plot 1. Secondary flowering was observed in Plot 2 for two culms, which flowered in May and bore three new shoots with inflorescences alone in mid-July 2006. However, fertilization of seeds did not take place in Plot 2. In Plot 3, there was no secondary flowering on existing culms, but 47 new shoots with inflorescences alone were observed in June 2007.

Table 2. The number of preceding flowering culms for each study plot.

Status for the major flowering year	Plot1	Plot2	Plot3
Vegetative	47	1	97
Flowering	247	5	52

Preceding flowering culms were observed in all the study plots, and appeared on both flowering and vegetative culms in the major flowering year (Table 2). The size of preceding flowering culms was significantly larger than both flowering and vegetative culms for all study plots (p<0.01) (Fig. 3).

The census of Plot 1 for 2005 revealed that all culms that had flowered once were dead, and there was no flowering after the major flowering year (Fig. 1b).

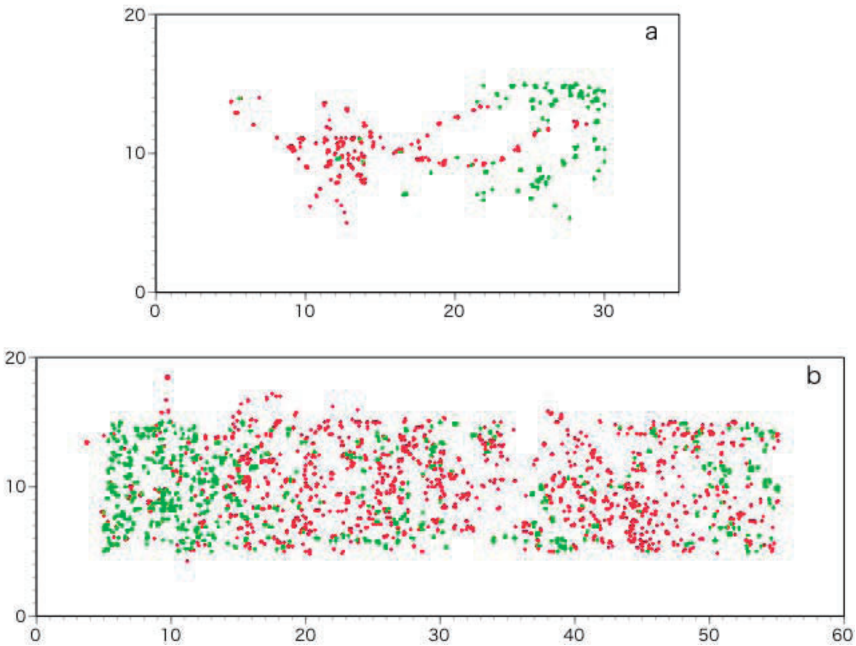

Fig. 2. Culm positions in Plot2 (a) and Plot3 (b) in 2006. Scales are given in meters. Red circle, flowering culm; green, vegetative culm

Discussion

A partial flowering, which precedes the gregarious flowering, has been reported for a couple of dwarf bamboo species (Nishiwaki & Makita, 1998; Kobayashi, 2000; Makita *et al*., 1988, 2004), but whether a single culm flowered twice in consecutive years, or different culms flower once in different years had not been determined. The two-year consecutive flowering on the same culm for *S. cernua* is a major finding of this study. Moreover, significantly larger culms tend to flower prior to the major flowering year. Yamazaki & Nakagoshi (2005) reported a similar result for *S. kurilensis*, where the living culm height was lower than dead culm height, indicating taller mature culms had flowered and died. These results suggest that size at maturation of the culm is one of the pre-requisites for the flowering of *S. cernua.*

Preceding flowering in dwarf bamboo species was reported along with the secondary flowering in small areas after a gregarious flowering year (Nishiwaki & Makita, 1998; Kobayashi, 2000; Makita *et al*., 1988, 2004). However, we observed no secondary flowering after the major flowering year in Plot 1. Regardless of the flowering year and frequency, all culms that had flowered in Plot 1 were dead and regenerated culms (Kobayashi & Nomura, 2001) were not observed until 2006. On the other hand, secondary flowering was observed in July of the major flowering year in Plot 2 and in June of the subsequent year in Plot 3.

The flowering season of *S. cernua* in Sapporo is primarily mid-May. In this study, we observed a secondary flowering in mid-July in a small flowering patch (Plot 2). The other two study sites produced seeds after the flowering in mid-May, but Plot 2 did not produce any seeds from the first flowering. This may indicate a relationship between fertilization and the potential to produce inflorescences; however, a quantitative study of seed production may be necessary to confirm this relationship.

Within the flowering area, approximately 40 to 60% culms were vegetative culms and did not flowered. This phenomenon has also been reported for mass-flowering of *S. kurilensis* (Makita, 1992; Makita *et al*., 2004).

We have also observed other sporadic flowering sites of *S. cernua* adjacent to these study sites from 2003 to 2006. The size of these flowering patches are 294 m^2, 868 m^2, and 958 m^2, which are similar to the size of Plot 1 (625 m^2) and Plot 2 (250 m^2). We could also assume expansion of underground rhizome connections of flowering culms from the culm position map of Plot 1 (Fig.1a) and Plot 2 (Fig. 2a) because Plot 3, the largest flowering area (1600m^2), was twice as large as the second largest flowering patch observed in the surrounding area. However, the location of flowering culms in Plot 3 shows a low density of flowering culms at approximately 35 m in the x-axis (Fig. 2b). If the unit of sporadic flowering of *S. cernua* is between 250 m^2 and 1000m^2, Plot 3 might be assumed to be two flowering patches joined at the middle of the plot.

Synchronous flowering units have been shown to be a genetic trait for *P. pubescens*, another monocarpic bamboo species (Isagi *et al*., 2004). Whether the sporadic flowering unit for *S. cernua* has a genetic basis can be elucidated using genetic markers, and this will form the basis of our next study.

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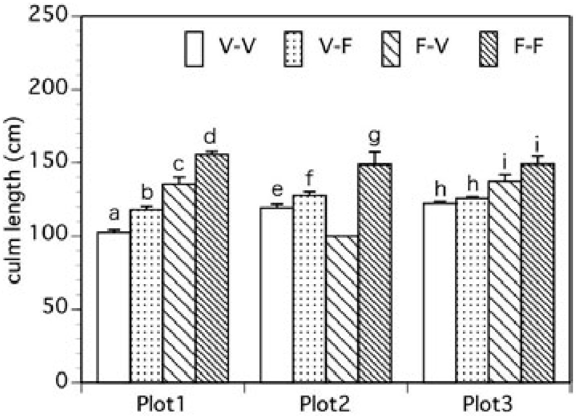

Fig. 3. Average culm length of different flowering status for each study plot. Standard errors are given in bars. Small case letters indicate significant difference by *t*-test (p<0.01), calculated independently for each study plot. V-V, vegetative for two years; V-F, flowering culm without preceding inflorescence; F-V, vegetative culm with preceding inflorescence; F-F, 2-year sequential flowering culm
No statistical test was carried out for status F-V in Plot2, where only a single culm was observed.

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オクヤマザサ部分開花集団における開花稈の動態

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要 旨

一回結実性植物として知られているササは、数十年に一度一斉開花し枯死する。ササにおける開花の範囲は、部分開花から大面積にいたるまでさまざまである。本研究では北海道の林床に広く分布するオクヤマザサ（*Sasa cernua*）の部分開花集団を対象に稈単位の詳細な位置図と開花の有無を調査した。調査を行った３プロットすべてにおいて開花の前年に部分的な開花があり、開花年には前年開花で枯死しなかった稈が再び開花する現象が見られた。つまり稈単位で開花性の調査を行うことによって、同一稈が連続して２年間咲くという事実が初めて明らかになった。また、前年開花を行う稈のサイズは行わない稈にくらべて有意に大きかった。これらの結果から、オクヤマザサの開花には稈サイズがなんらかの影響を及ぼしていることが示唆された。開花後の追跡調査では、過去に一度でも開花した稈はすべて枯死しており、再生稈は認められなかった。結実しなかった小面積の開花パッチでは開花同年の７月に再開花が認められた。また、開花翌年に花穂のみからなる新たな稈の発生が認められた。本調査地におけるオクヤマザサ部分開花の範囲は、周辺の開花集団も含めて約 250 ～ 1000m² と推定された。

キーワード：一回結実性植物、ササ属、開花同調、部分開花、林床性ササ

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