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REGULAR PAPER

Genets of dwarf bamboo do not die after one flowering event: evidence from genetic structure and flowering pattern

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Abstract Dwarf bamboos in the genus *Sasa* are believed to be long-lived, synchronously flowering, and monocarpic plants. However, the monocarpy of dwarf bamboo has not been confirmed, because whether all ramets within one genet flower at the same time cannot be determined without differentiating the genetic structure among ramets. This study aims to evaluate the reproductive traits of *Sasa pubiculmis* by verifying the monocarpy and physiological integration between flowering ramets and non-flowering ramets during a 4-year flowering period. One genotypically identified genet, which covered an area of approximately 3 ha, had both flowering and non-flowering patches of ramets during the 4-year flowering period (2004–2007). A fraction of the flowering genet remained non-flowering during the 4 years of observation, and did not die after mass flowering. Flowering ramets were physically connected to non-flowering ramets via rhizomes, and assimilated ^{13}C was allocated from non-flowering ramets to flowering ramets. Consequently, we clarified that this dwarf bamboo potentially has polycarpic reproductive traits rather than monocarpic, and a genet can keep rhizomes and non-flowering patches alive to sustain the organism after mass flowering.

Keywords AFLP · Clonal plant · Long-lived species · Mass flowering · Monocarpy · Reproductive traits

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Introduction

Sasa, the dwarf bamboo that forms extensive and dense populations that undergo mass flowering followed by simultaneous death, have great impacts not only on the dynamics of forest ecosystems (Nakashizuka 1988; Wada 1993; Hiura et al. 1996; Abe et al. 2001) but also on their functioning (Fukuzawa et al. 2006; Sakai et al. 2006). Many hypotheses have been proposed to explain the evolution of this synchronized monocarpy in bamboo species, including predator satiation (Janzen 1976), parental competition (Simmonds 1980; Gadgil and Prasad 1984), climatic periodicity (Campbell 1985), and response to a fire cycle (Keeley and Bond 1999; commented on by Saha and Howe 2001). However, the synchronized monocarpy of *Sasa* has not yet been demonstrated in a strict sense because of the difficulty of identifying the individuality and the genetic structure of the population during flowering. While the genetic structure of a population of *Sasa senanensis* has been demonstrated once by amplified fragment-length polymorphism (AFLP) analysis, which

showed one genet occurring over a distance of about 300 m (Suyama et al. 2000), no studies have been conducted on flowering populations. Monocarpy is relatively rare among long-lived plants, including *Sasa*, suggesting that monocarpy may be an evolutionary dead-end for long-lived species (Poorter et al. 2005). Therefore, if not all ramets of one genet flower at the same time, and not all die after flowering or fruiting, then we must reconsider the life history traits of *Sasa* as polycarpic.

During a flowering and a fruiting period, reproductive organs operate as resource sinks, and reproductive organs obtain carbon resources from the nearest vegetative organs (Mooney 1972; Stephenson 1981; Obeso 2002; Miyazaki et al. 2007). *Sasa* species are clonal plants, thus the physiological integration among intraclonal ramets enables a genet to integrate local heterogeneity with resource availability (Hartnett and Bazzaz 1983; Alpert and Mooney 1986; Evans 1992; Kelly 1995; Saitoh et al. 2002, 2006). Since production of seeds and flowers of *Sasa* requires huge resources at mass flowering, the source–sink balance at mass flowering will be different from that during the non-flowering period. Consequently, flowering ramets might be supported by translocation of resources from the connected non-flowering ramets.

In the present study, we identified the genetic structure of *Sasa pubiculmis* Makino subsp. *pubiculmis* by means of an AFLP technique (Vos et al. 1995) and investigated the flowering patterns and the rate of seed set of one genet during four growing seasons (2004–2007). In addition, we excavated the rhizomes to clarify whether flowering ramets were connected directly to non-flowering ramets. After the excavating survey, we conducted tracer experiments using $^{13}CO_2$ to trace the movement of current photosynthates between flowering ramets and non-flowering ramets. Finally, we discussed the reproductive traits of this dwarf bamboo, especially the existence or non-existence of monocarpy.

Materials and methods

Study species

The target species was *Sasa pubiculmis* Makino subsp. *pubiculmis*. The voucher specimens are housed in the University Museum, the University of Tokyo. The mean density of the ramets in this study plot was 48.2 m^{-1} (Y.M. et al., unpublished data). The *Sasa* group containing *S. pubiculmis* has been categorized to have a flowering pattern with periodic gregarious flowering at approximately regular intervals, to be generally monocarpic, but still in some cases with partial survival of weakened rhizomes (Campbell 1985).

Study site and samples

The study site was in the Tomakomai Experimental Forest of the Field Science Center for Northern Biosphere, Hokkaido University (TOEF; 42°40′N, 141°36′E, 2,715 ha), in northern Japan. The monthly mean air temperature ranges from −3.2 to 19.1°C, and the mean annual precipitation is 1,450 mm (Hiura 2005). Snow cover reaches a depth of 50 cm from December to March. The study site was a deciduous broad-leaved forest stand dominated by *Quercus crispula* Blume, *Acer mono* Maxim., *Sorbus alnifolia* (Sieb. Et Zucc.) C. Koch and *Tilia japonica* (Miq.) Simonkai (Hiura et al. 1998; Hiura 2001). *Sasa yahikoensis*, *Sasa nipponica, Sasa kurilensis* and *Sasamorpha borealis* are distribute in the study site in addition to the study species. The forest floor was commonly covered with *Dryopteris crassirhizoma*, *Maianthemum dilatatum* and *Smilacina japonica* (Hasegawa and Kudo 2005). This forest was formed on 2-m-deep volcanogenous regosols that accumulated from the eruptions of Mt. Tarumae in 1669 and 1739, and the depth of the A-horizon is 0–6 cm (Shibata et al. 1998). Therefore, the light, soil and topographic conditions seemed to be uniform in the research plot at the start of this study.

To investigate the flowering patterns of *S. pubiculmis*, we conducted a location survey and set up a research plot covering the area where flowering was occurring (approximately 3 ha; described in Fig. 1) and marked each intersection point of a 20 × 20 m grid within the plot using steel pipes in early June 2004. There were no large canopy gaps in the research plot in early June 2004 when the plot was set up, although two canopy gaps (around 10 m in diameter) were created by a large typhoon in 18 September 2004. We observed the flowering status of the approximately 200 ramets surrounding the points (approximately 2 × 2 m). The flowering status was observed from 2004 to 2007 and the status at each point was classified into three categories: (1) an intensively flowering patch in which all ramets were flowering, (2) a mixed flowering patch containing both flowering and non-flowering ramets (usually existing around the intensively flowering patch), (3) a non-flowering patch in which no ramets were flowering. In the research plot, we took three fresh leaf samples for DNA extraction from three live ramets at the intersection points of the grid in 2004. In a mixed flowering patch, we took samples from both flowering and non-flowering ramets. Flowering ramets sometimes did not flush with new leaves and, in such cases, we collected paleae from the flowering ramets instead of leaves. The leaf and paleae samples were kept at 4°C until DNA extraction. Since analysis of leaf and palea samples from the single flowering ramet (which retained leaves) showed no tissue-specific AFLPs, artifacts from tissue-specific AFLP fragments were not considered in our analysis.

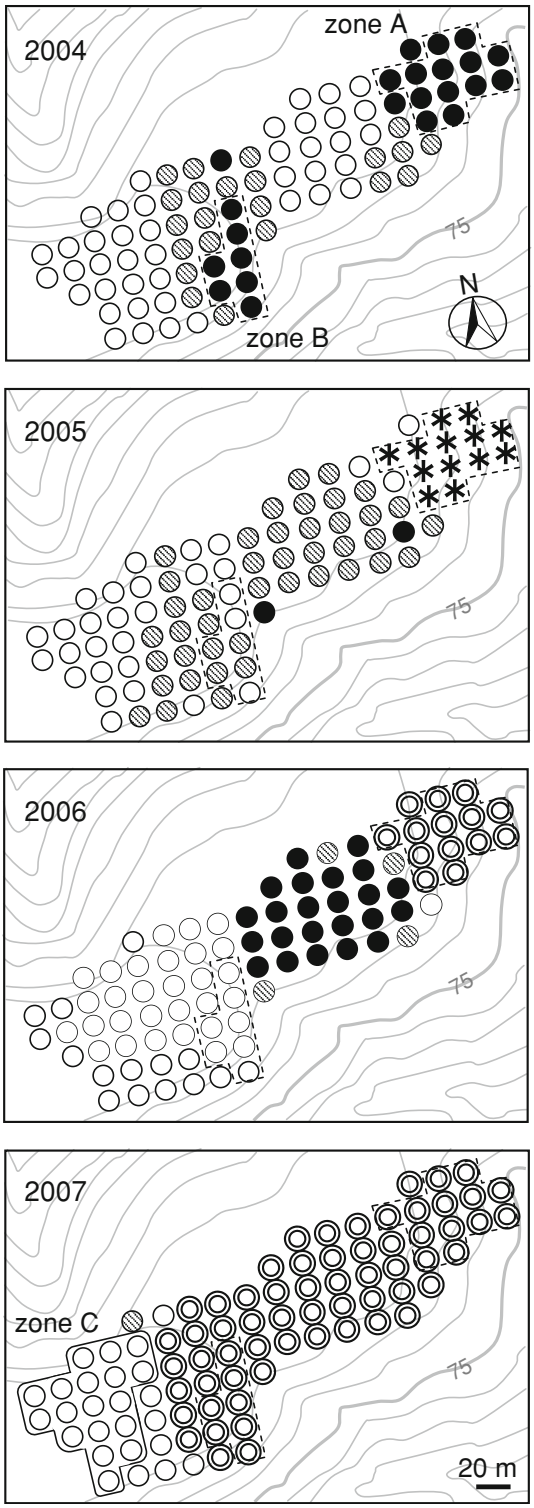

Fig. 1 Maps of the flowering pattern in one genet of *Sasa pubiculmis* from 2004 to 2007. *Filled circles* Intensively flowering patches, *open circles* non-flowering patches, *shaded circles* mixed flowering patches, *double circles* patches containing regrown ramets sprouted spikelets directly from the ground. *Asterisks* Patches where above-ground parts died after intensive flowering. *Dotted lines* enclose zones A and B, a *solid line* represents zone C

To identify direct connections between the flowering and the non-flowering ramets, we excavated the rhizomes within a 1 × 1 m area in 2004 using shovels and a small backhoe at a point with mixed flowering, and unraveled the rhizomes. Genetic identities of all the ramets within this area were analyzed by AFLP.

DNA extraction and AFLP analysis

DNA extracted using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) from 50 mg leaf or palea samples was stored in Tris-EDTA buffer. AFLP analysis was carried out as described by Vos et al. (1995) using an AFLP Core Reagent Kit (Invitrogen, Carlsbad, CA) and an AFLP Plant Mapping Kit (Applied Biosystems, Foster City, CA). Selective amplification was carried out with three sets of *Mse*I (M-) and *Eco*RI (E-) primers (M-CTC/E-ACT, M-CTG/E-AAC, and M-CTT/E-ACG; Suyama et al. 2000). All reactions were performed using a GeneAmp PCR system 9700 (Applied Biosystems). AFLP profiles were obtained with a 3100-Avant Genetic Analyzer and the GeneMapper 3.5 software (Applied Biosystems) and were compared for the presence or absence and intensity of fragments.

Seed production

Seed set (i.e., the proportion of flowers that set seed) was calculated from sampling of 50 spikelets based on the estimated mean numbers of flowers per terminal spikelet (=104). We collected these 50 spikelets randomly from an intensively flowering patch.

^{13}C tracing and analysis

The ^{13}C tracing experiment was conducted following the procedures described in Hasegawa et al. (2003) and Miyazaki et al. (2007) during 18–20 May 2007, when flowering ramets were increasing in size. To investigate whether each flowering ramet is supported by non-flowering ramets, we selected a unit of ramets connected with rhizome as follows: (1) a flowering ramet connected to another non-flowering ramet ($n = 10$), (2) a non-flowering ramet connected to another non-flowering ramet ($n = 10$). These two experimental units were excavated from the study site and transplanted to planters 1 day before the experiment. $^{13}CO_2$ was provided from the non-flowering ramet in each unit, and we measured the atom % of ^{13}C of the connected ramet.

A ramet was enclosed in a transparent plastic bag (volume ~5 L) and sealed, and this was then used as a simple chamber. $^{13}CO_2$ was produced by reacting $Ba^{13}CO_3$

(99% ^{13}C; Shoko, Tokyo, Japan) with HCl, and was injected in amounts of 5 mL into each bag. Each bag was retained for two successive days, from 0900 hours on 18 May to 1300 hours on 20 May, and the $^{13}CO_2$ generation was carried out twice, at 0900 hours on 19 and 20 May. After 52 h exposure, the rhizomes between the ramets, the ramets that had been exposed to $^{13}CO_2$ and the adjacent ramets were cut off. During this experiment, the average air temperature was 10.0°C and the average relative humidity was 82% (Japan Meteorological Agency). Samples were dried at 60°C for 48 h and ground to a fine powder in a blender (WB-1; Osaka-Chemical, Osaka, Japan). The abundance of ^{13}C was determined using an automated stable isotope ratio mass spectrometer (INTEGRA-CN; Sercon, Cheshire, UK). The abundance of ^{13}C was indicated in atom %. Atom % of ^{13}C was calculated as follows:

$$\text{atom}\% = \frac{\text{amount of } ^{13}\text{C}}{\text{amount of } ^{12}\text{C} + \text{amount of } ^{13}\text{C}} \times 100$$

The increment of ^{13}C in the connected ramets from controls was analyzed by the Mann–Whitney *U* test, comparing atom % of ^{13}C of the connected ramets with atom % of ^{13}C of the control ramets. The control ramets were collected 1 day before the experiment from around the excavation point of the experimental units. The Mann–Whitney *U* test was performed with Stat View Version 5.0 (SAS Institute, Cary, NC).

Results

Only one genet flowered during the study period (in an area of approximately 3 ha). The observed numbers (and sizes) of fragments by AFLP analysis were 15 (57–436 bp), 8 (53–421 bp) and 13 (52–435 bp) using the three primer pairs M-CTC/E-ACT, M-CTG/E-AAC and M-CTT/E-ACG, respectively. The flowering genet had both flowering and non-flowering patches during the flowering period in 2004, and this flowering pattern was also found in the following 3 years (Fig. 1).

Patches of intensive flowering (filled circles) were separated by non-flowering patches (open circles) in 2004 (Fig. 1). Mixed flowering patches were also present, in which flowering and non-flowering ramets coexisted as scattered ramets (shaded circles), around the intensively flowering patches. In 2004, the ramets in one intensively flowering patch (zone A, enclosed by a dotted line) died, and the dead ramets in 2005 are indicated by asterisks; in contrast, the ramets in another intensively flowering patch (zone B, enclosed by a dotted line) were still alive in 2005. In 2006, we found new non-flowering ramets in zone A, which had regrown from the rhizomes of the ramets that had flowered in 2004 and were thought to be dead in 2005 (actually only the above-ground part died, Fig. 2). In 2006, regrown ramets sprouted spikelets directly from the ground (double circles). Furthermore, in 2007, new flowering ramets appeared directly from the ground as spikelets in the area where ramets flowered at least once during the last 3 years (Fig. 1). Although the majority of the ramets within this genet flowered, the ramets in zone C (enclosed by a solid line in Fig. 1) did not flower and did not die during the 4 years of our study.

No seed set was observed in 2004, 2005 and 2007, but a low seed set (0.10%) was observed in 2006 in the intensively flowering patch.

The excavating survey revealed that several rhizomes of the flowering ramets were connected to non-flowering ramets, and that all these ramets belonged to the same genet according to the AFLP analysis. The non-flowering ramets that were connected to the flowering ramets did not die after the flowering period of the flowering ramets. Assimilated ^{13}C was transported from the non-flowering ramet to the flowering ramet via rhizome, whereas no assimilated ^{13}C was transported from the non-flowering ramet to the non-flowering ramet via rhizome (Table 1).

Discussion

Individuals in populations of *Sasa* and some bamboo groups have been considered to flower synchronously (reviewed in Janzen 1976). However, earlier reports

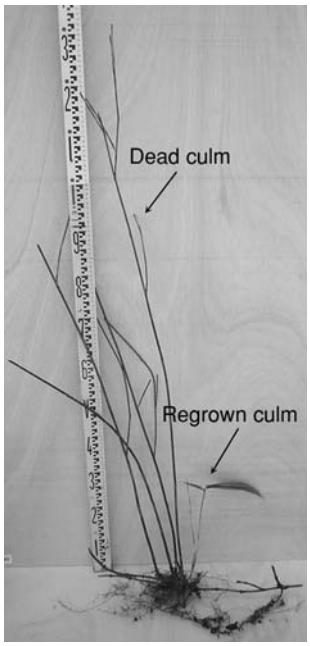

Fig. 2 Photograph of a rhizome and ramets sampled in zone A in 2006. The new ramet regrew from the rhizome of a ramet that had flowered in 2004 and then died

Table 1 Atom % of ^{13}C (mean ± SD, $n = 10$) in treated ramets (connected to non-flowering ramets to which ^{13}C was provided) and control ramets

Treatment and control	Atom % of ^{13}C
Non-flowering ramet	
Treatment	1.080 ± 0.0010
Control	1.080 ± 0.0011
Flowering ramet	
Treatment	1.117 ± 0.0282*
Control	1.081 ± 0.0012

Atom % of the flowering ramet group was significantly different ($P < 0.001$) from the control value according to the Mann–Whitney U test

* $P < 0.001$

describing flowering populations of *Sasa* (Nishiwaki and Makita 1998; Makita et al. 1988, 2004; Kobayashi and Nomura 2001; Kitamura and Kawahara 2007) did not determine whether flowering populations consisted of a single genet or several genets. Because *Sasa* forms extensive and dense populations by means of extended rhizomes and vigorous culm production, it is difficult to identify how many genets exist in a population, and how large an area is occupied by a single genet (Suyama et al. 2000). Our results clarify, for the first time, the genetic structure and the spreading area of a flowering population concurrently, and show that a flowering population covering several hectares consisted of a single genet of the dwarf bamboo *S. pubiculmis*.

Clonal plants exhibit physiological integration, in which new ramets remain connected to the parent plant and share its resources (e.g., water uptake via established rhizomes), thereby reducing the risks of establishing new ramets and enabling a genet to compensate for local heterogeneity in resource availability (Hartnett and Bazzaz 1983; Alpert and Mooney 1986; Evans 1992; Kelly 1995; Saitoh et al. 2002, 2006). During flowering and fruiting periods reproductive organs operate as resource sinks, and reproductive organs obtain carbon resources from the nearest vegetative organs (Mooney 1972; Stephenson 1981; Obeso 2002; Miyazaki et al. 2007). Flowering ramets thus receive support via translocation from connected non-flowering ramets. In the case of *S. pubiculmis*, several rhizomes of flowering ramets were connected to non-flowering ramets, and the flowering ramets were provided with carbon from the connected non-flowering ramets (Table 1) by physiological integration. *S. pubiculmis* may therefore compensate for the large cost of reproduction by connecting non-flowering ramets.

Many bamboo ramets have been believed to die simultaneously after mass flowering, especially when seed production is heavy (Campbell 1985). The reason proposed for why the parent ramets die was that there is heavy selection for producing a large seed crop, and only a small amount of resources could be saved to reestablish the adult after such mass seeding (Janzen 1976). Despite the very low seed production in this study, the above-ground parts of the intensively flowering patch in 2004 (Fig. 1, zone A) died after their flowering period. This may have been due to insufficient resources resulting from the relatively high reproductive cost of flowering without seed production. If heavy seed production occurred, resources in the rhizome might be depleted thus increasing the possibility of death of the whole organism. In order to confirm this phenomenon, it may be necessary to do a quantitative study of the cost of reproduction.

Dwarf bamboo has been categorized as having a monocarpic flowering pattern (Janzen 1976; Campbell 1985). Most mass flowering species are polycarpic and can flower and fruit multiple times during their life span (Silvertown 1980). Monocarpy is relatively rare among long-lived plants that grow in stable habitats, suggesting that monocarpy may be an evolutionary dead-end for long-lived species (Poorter et al. 2005). In this study, we found that not all ramets in a single genet are strictly programmed to flower simultaneously. Furthermore, even after the flowering period, the whole organism did not necessarily die off. These results do not fall within the definition of monocarpy in a strict sense and suggest the possibility that *S. pubiculmis* actually has a polycarpic reproduction system. The genets may not die at the flowering event, which continues for a few years, and may survive and repeat periodical flowering events. When flowering occurs over a larger area at a population level (gregarious flowering), multiple genets are potentially included in the flowering area. Thus, the possibility remains that our findings may apply only in the case of sporadic flowering (McClure 1966; Makita and Konno 1989). Since our hypothesis that *S. pubiculmis* has a polycarpic reproductive system was constructed only from the analysis of one genet at sporadic flowering, it is necessary to analyze the genetic structure of other gregarious flowering population for further generalization of this hypothesis.

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