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Mass-flowering of Cultivated Moso Bamboo, *Phyllostachys edulis* (*Poaceae*) after More Than a Half-century of Vegetative Growth

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Bamboos are long-lived monocarpic species of *Poaceae*; few studies have assessed their entire lifespan from seedling to the reproductive phase. In July 2021, moso bamboo, *Phyllostachys edulis* (Carrière) J.Houz., cultivated from seedlings for more than half century, mass-flowered at the Kamigamo Experimental Station at Kyoto University, Kyoto Pref. and the Fuji Bamboo Garden, Shizuoka Pref., Japan. We observed the rare phenomenon and estimated the age of these bamboo stands at the time of flowering to be 66 and 67 years, respectively, based on historical records and interviews with staff at both facilities. From these and previous studies, we found that moso bamboo clones with a monocarpic life history have a lifespan of 66–69 years in Japan. However, mass-flowering has never been reported in naturally occurring moso bamboo forests across Japan over the approximately 300 years since its introduction from China. This suggests that life history traits, including reproductive characters might have some variation in moso bamboo.

Key words: Bamboo, flowering, lifespan, long-term experiment, monocarpic reproduction, *Phyllostachys edulis*, *Phyllostachys pubescens*, stone monument.

Bamboos (*Poaceae*) are long-lived plants with a monocarpic life history (Janzen 1976). The length of their lifespan presents challenges for tracking individuals from the seedling phase through to reproduction. Thus, their lifespan (or flowering interval) is often estimated from historical records (Janzen 1976, Veller et al. 2015, Zheng et al. 2020). For example, *Phyllostachys nigra* (Lodd. ex Lindl.) Munro var. *henonis* (Mitford) Rendle and *P. bambusoides* Siebold & Zucc. have estimated flowering intervals of approximately 120 years in Japan (Shirai 1911, Kawamura 1911a, b, c, 1912, 1927, Kobayashi et al. 2022), but the true lifespan has only been quantified a few times (Table 1); long-term experiments are necessary to address this question quantitatively (Konno 1937).

Moso bamboo, *P. edulis* (Carrière) J.Houz. [= *P. pubescens* (Pradelle) J.Houz., *P. heterocycla* (Carrière) Matsum. var. *pubescens* (J.Houz.) Ohwi], is native to China and is widely accepted to be introduced to Japan in the 18th century. Due to its history, a single clone is indicated to be widely distributed across Japan (Isagi et al 2016). This bamboo generally exhibits a sporadic flowering pattern in the field, in which some of the culms in a bamboo forest flower (Kasahara et al. 1970, 1980, Isagi 2010, Kobayashi and Kobayashi 2019). Some researchers believe that the moso bamboo in Japan will eventually mass-flower (e.g., Kasahara et al. 1970, 1980, Kasahara 1999). In any case, clarifying the life history traits in relation to the sexual reproduction of moso bamboo is an interesting research topic not only for understanding the evolutionary background of bamboos but also for bamboo resource management. Long-term monitoring started at the beginning of the 20th century using seedlings collected at times of sporadic flowering in moso bamboo forests. To date, seedlings obtained from sporadic flowering events in 1912 and 1930 in Yokohama, Kanagawa Prefecture, which have since become healthy stands, exhibited mass-flowering across Japan mainly in 1979 and 1997, respectively, showing a lifespan of 67 years (e.g., Watanabe et al. 1982, Kasahara 1999, Shibata 1999, 2002). In the later flowering event, Isagi et al. (2004) assessed a moso bamboo stand at Akanuma Experimental Forest Station, Saitama Prefecture that exhibited a mass flowering for three years (1997–1999). They showed that the flowering culms forming the stand belonged to two genets with distinct flowering intervals of 67 and 69 years, based on amplified fragment length polymorphism analysis. These limited reports show that there are monocarpic clones of moso bamboo with lifespans of around 67 years in Japan, but the accumulation of more data is essential. Here, we report the third and fourth cases of successful determination of the lifespan of monocarpic moso bamboo in Japan, along with detailed observations.

Materials and Methods

Site description

Study sites were located at the Kamigamo Experimental Station (KA) at Kyoto University, Kyoto Prefecture, and the Fuji Bamboo Garden (FU), Shizuoka Prefecture, Japan (Table 2). Mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) over the lifetime of the stand were determined based on data obtained from Nakagawa et al. (2020) for KA and from the nearest Automated Meteorological Data Acquisition System (AMeDAS) station of the Japan Meteorological Agency for FU. At both sites, some moso bamboo stands had been established by planting and this study targeted one moso bamboo stand in each site (Table 3, ID1 and ID12). The planted area was 5 × 5 m at KA and 3 × 10 m at FU (Figs. 1a, e, 2). Both stands have been managed, including selective logging of dead and older culms, but neither has been fertilized. Both stands underwent a single transplantation within the same station or garden, due to facility migration. Transplanting occurred in 2003 at KA and in 1971 at FU. Neither stand has ever been observed to flower.

Historical records and interviews

We used ledger records, literature, a stone monument, and interviews with station staff to estimate the age of the stand at KA (Table 3, ID1). Given these sources, the stand is believed to have originated from seedlings that germinated in 1956 (Fig. 1b). The number of founding seedlings is unknown, but seeds were obtained from three flowering culms in June 1955 from a managed bamboo forest in Kamigamo Nikenjaya, Kita-ku, Kyoto, Kyoto Prefecture (35°04′34″N, 135°45′54″E) (Ueda 1961, Kasahara et al. 1970). We note one discrepant ledger record for KA, showing that the stand originated from seeds germinated in 1958, but by combining this information with other available records, including the stone monument, we believe this discrepant record

Table 1. Examples of bamboo species (*Poaceae*: *Poales*) tracked from seedling to flowering under cultivation.

Species	Seedling emergence		Mass flowering records		Years to flowering[2]	Related references
	Year	Location[1]	Year	Location[1]		
Phyllostachys edulis (as *P. pubescens*)	1913	Hassaka-cho, Midori-ku, Yokohama, Kanagawa Pref., Japan	1979	Kamigamo Experimental Station, Kyoto Pref., Japan Nakayama-cho, Midori-ku, Yokohama, Kanagawa Pref., Japan Kanagawa Prefecture Natural Environment Conservation Center, Kanagawa Pref., Japan	67	Maeda (1917) Okamura (1980) Kasahara et al. (1980) Watanabe et al. (1982)
P. edulis (as *P. pubescens*)	1931	Miyata-cho, Hodogaya-ku, Yokohama, Kanagawa Pref., Japan	1997–1999	Kamigamo Experimental Station, Kyoto Pref., Japan Akanuma Experimental Forest Station, Saitama Pref., Japan The University of Tokyo Chiba Forest, Chiba Pref., Japan The University of Tokyo Tanashi Forest, Tokyo Pref., Japan Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	67, 69	Konno (1937) Nagao and Ishikawa (1998) Suzuki and Ide (1998) [3] Ide and Suzuki (1998) [3] Kasahara (1999) Shibata (1999) [3] Shibata (2002) [3] Isagi et al. (2004) Kobayashi (2017)
P. edulis	1955	Oharano, Nishikyo-ku, Kyoto, Kyoto Pref., Japan	2021	Fuji Bamboo Garden, Shizuoka Pref., Japan	67	Takagi (1957, 1960, 1965) Kasahara et al. (1970) This study
P. edulis	1956[4]	Nikenjyaya, Kita-ku, Kyoto, Kyoto Pref., Japan	2021	Kamigamo Experimental Station, Kyoto Pref., Japan	66	Ueda (1961) Kasahara et al. (1970) This study
Melocanna baccifera	1961[5]	Puerto Rico	2008	Zhushan, Nantou Co., Taiwan	48	Lu and Chen (2009) Shibata (2010)
M. baccifera	1962[5]	Bangladesh	2009	Shirahama-cho, Nishimuro-gun, Wakayama Pref., Japan	48	Shibata (2010)

[1]Locations are provided using current information.
[2]Years from seed to seed.
[3]These literature records reported sporadic flowering in bamboo stands of the same clonal origin at the Tsukuba Forest Research Institute and the Tochigi Forestry Research Center. As we could not confirm whether each was ultimately mass-flowering or not, they are excluded from the Table 3.
[4]Kamigamo Experimental Station also had a ledger record of "1958 seedlings" (see details in the text).
[5]The year was estimated from the flowering pattern of this species (Shibata 2010).

to be incorrect.

The age of the stand at FU (Table 3, ID12) was estimated using ledgers, the literature, and interviews with garden staff. The number of founding seedlings is unknown, but seeds were collected in July 1954 from flowering culms in Oharano, Nishikyo-ku, Kyoto, Kyoto Prefecture (approximately 34°57′51″N, 135°

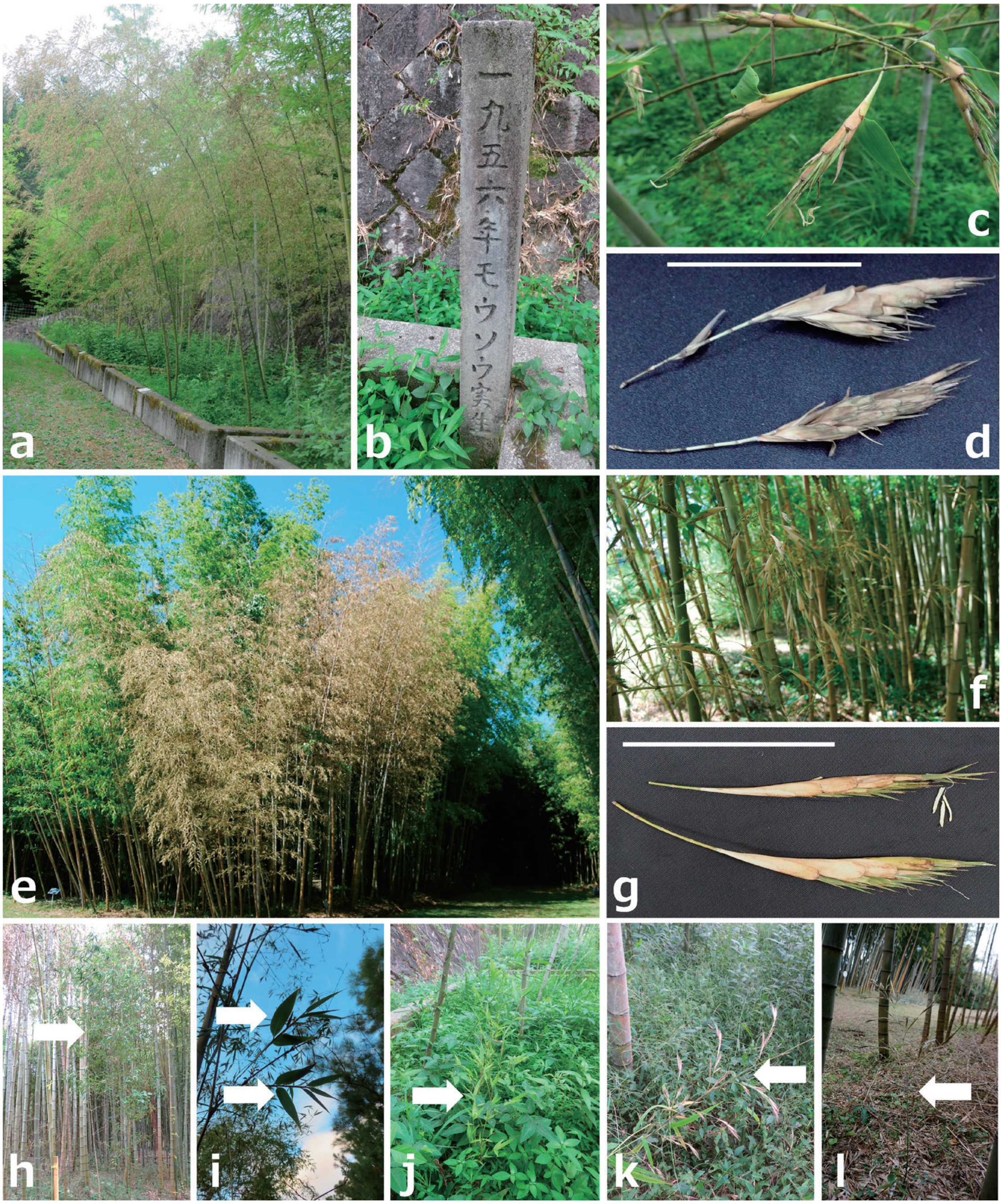

Fig. 1. Photographs of the study sites, bamboo stands, and reproductive structures. a. Flowering bamboo stand. b. Stone monument inscribed with “Moso bamboo seedling from 1956”. c, d. Spike inflorescences from the Kamigamo Experimental Station (KA). e. Flowering bamboo stand. f, g. Spike inflorescences from the Fuji Bamboo Garden (FU). Both stands flowered simultaneously in July 2021. h. Twenty-one percent of the living culms at FU did not flower as arrowed. i. A number of branches at KA did not bear reproductive organs, as arrowed, during the study period. j–l. Dwarf shoots (arrowed) emerged. j, k. Before flowering at both study locations. l. Culms after flowering at FU. Scale bars = 50 mm (d, g). Photos a–g and j were taken in July 2021 and photos h, i, k and l were taken in October 2021.

Table 2. Locality and climatic factors of study sites. Mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) were calculated using data from 1955–2020 obtained from the AMeDAS station nearest to the study site (Japan Meteorological Agency) for Fuji Bamboo Garden (FU) and from Nakagawa et al. (2020) for Kamigamo Experimental Station (KA). Means ± standard deviations are shown. Minimum and maximum values are shown in parentheses.

Site	Code	Latitude	Longitude	Elevation (m)	MAT (°C)	MAP (mm)
Kamigamo	KA	35°04′13″N	135°45′53″E	130	14.6 ± 0.642 (13.5–16.6)	1639.2 ± 278.3 (1073.0–2220.5)
Fuji	FU	35°09′46″N	138°53′15″E	155	15.8 ± 0.673 (14.6–17.3)	1866.1 ± 327.1 (1104.0–2750.0)

40′29″E) and germinated in April 1955 (Takagi 1957, 1960, 1965, Kasahara et al. 1970). Seedlings were transplanted to the garden from the Kyoto area in 1958.

Field survey

We recognized flowering on 21 July 2021 in both stands of KA and FU and conducted field surveys from July 2021 to January 2022. We recorded culm diameter at breast height (DBH), culm height from the ground, culm age, and culm position within each stand. Culm age was categorized as 1, 2, and ≥ 3 years based on the presence of white wax on the node surface and the overall branching pattern (Ueda 1960). All living culms were classified as flowering or non-flowering culms. The emergence and flowering status of dwarf shoots were also observed.

Results

Culm number, culm dimensions, and flowering status at the two study sites (KA and FU) are provided in Table 4. Overall, 100% (19/19) of all culms at KA flowered, whereas 79% (62/78) flowered at FU. The majority of flowering culms was over two years old , with a few that had emerged during spring 2021. At both sites, the majority of leaves had already been shed and the floral organs had formed, although some branches without inflorescences were observed at KA (Fig. 1i). We also observed some inflorescences with small leaves (–3 cm in length) in July (Fig. 1c, f), most of which had abscised by October, and these inflorescences appeared to produce some mature seeds (Fig. 1d, g). For preliminary data, at KA, 3700 mature seeds (4350 inflorescences) were estimated in laboratory work from a 2-year-old culm (DBH = 3.3 cm) in November 2021. At FU, 94 mature seeds were collected in filed work from 11 culms in October–November 2021. The surfaces of flowering culms remained green throughout the study period and did not show signs of mortality. Dwarf shoots were observed at both sites (Fig. 1j, k), with a mean (± SD) height of 0.87 ± 0.36 m (n = 6) at KA and approximately <1 m (n = 3) at FU. At KA, 1-year-old dwarf shoots were not flowering in July (Fig. 1j), but began flowering until October (Fig. 1k). At FU, 1-year-old dwarf shoots began flowering in July. A non-flowering dwarf shoot emerged in August–October 2021 and then flower buds were formed until 2022 January (Fig. 1l).

Discussion

We obtained clear evidence of mass-flowering of moso bamboo at two different experimental sites in Japan. Based on available evidence, the ages of these moso bamboo stands at the time of flowering were 66 years for KA and 67 years for FU. To our knowledge, only two other records of monocarpic moso bamboo have been published, namely 67 and 69 years (Watanabe et al. 1982, Nagao and Ishikawa 1998, Suzuki and Ide 1998, Kasahara 1999, Shibata 1999, Isagi et al. 2004) (Table 1). Our lifespan estimates were very consistent with other reports from Japan. These results showed that monocarpic moso bamboos in Japan have a flowering cycle of 66–69 years. Note that at

Table 3. Seedling emergence (germination) year, planting location, and additional information for all moso bamboo (*Phyllostachys edulis*) planted at the Kamigamo Experimental Station (KA) and the Fuji Bamboo Garden (FU).

ID	Location of seed origin	Seed collection year	Seedling emergence	Planting location	Related references	Additional information
1	Kamigamo Nikenjyaya, Kita-ku, Kyoto, Kyoto Pref., Japan	1955	1956	KA	Ueda (1961) Kasahara et al. (1970) This study	Three flowering culms
2	Tachibana-cho, Anan, Tokushima Pref., Japan	1955	1956	KA	–	
3	Fushimi-ku, Kyoto, Kyoto Pref., Japan	1957	1958	KA	–	One flowering culm in Shimazu Bamboo Forest Station Four seedlings
4	KA	1979	1980	KA	Maeda (1917)[1] Watanabe et al. (1982)[1]	
5	Nakayama-cho, Midori-ku, Yokohama, Kanagawa Pref., Japan	1979	1980	KA	Maeda (1917)[1] Okamura (1980)[1]	
6	KA	1997	1998	KA	Shibata (1999)[1]	
7	Jiangsu Prov., China	1978	1979	KA	–	From Nanjing Forestry University The same clone was planted in Rakusai Bamboo Garden.
8	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	unknown	unknown[2]	KA	–	Rhizome "short" type Called *Seiyou-mouchiku* by Wakayama Farm
9	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	unknown	unknown[2]	KA	–	Stem "*akebono*" type Called *Himeakebono-mousou-chiku* by Wakayama Farm[3]
10	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	unknown	unknown[2]	KA	–	Called *Toumyo-chiku* by Wakayama Farm[3]
11	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	unknown	unknown[2]	KA	–	Fewer hairs on the culm surface Called *Ao-mousou* by Wakayama Farm
12	Oharano, Nishikyo-ku, Kyoto, Kyoto Pref., Japan	1954	1955	FU	Takagi (1957, 1960, 1965) Kasahara et al. (1970) This study	
13	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1967	1968	FU	-	*P. edulis* (Carrière) Houz. 'Tao Kiang'
14	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1968	1969	FU	-	Stem "*akebono*" type One seedling
15	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1968	1969	FU	-	Stem "*akebono*" type One seedling Smaller than ID8

Table 3. Continued.

ID	Location of seed origin	Seed collection year	Seedling emergence	Planting location	Related references	Additional information
16	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1968	1969	FU	-	Rhizome metamorph type One seedling
17	Midori-ku, Yokohama, Kanagawa Pref., Japan	1979	1980	FU	-	Nine seedlings
18	Lipu, Guilin District, Guangxi, China	1979	1980	FU	-	Four seedlings
19	Kamado, Gotemba, Shizuoka Pref., Japan	1987	1988	FU	-	Small-size One seedling
20	Kamado, Gotemba, Shizuoka Pref., Japan	1987	1988	FU	-	Nine seedlings
21	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1996	1997	FU	-	
22	China	1996	1997	FU	-	
23	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1997	1998	FU	-	
24	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1998	1999	FU	-	
25	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1999	2000	FU	-	Seeds obtained from culms that flowered simultaneously in 1974 after 25 years of vegetative growth
26	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1999	2008	FU	-	Seeds frozen for 8 years
27	Takaragi-honcho, Utsunomiya, Tochigi Pref., Japan	1997	2008	FU	-	Seeds frozen for 10 years
28	Shimowada Shinden, Susono, Shizuoka Pref., Japan	2007	2008	FU	-	
29	Inno, Gotemba, Shizuoka Pref., Japan	2012	2013	FU	-	
30	Izu, Shizuoka Pref., Japan	2016	2017	FU	-	
31	Kamado Washinden, Gotemba, Shizuoka Pref., Japan	2016	2017	FU	-	
32	Kamado, Gotemba, Shizuoka Pref., Japan	2017	2018	FU	-	
33	Kamado, Gotemba, Shizuoka Pref., Japan	2017	2018	FU	-	Seeds obtained from *P. edulis* (Carrière) Houz. 'Tao Kiang'
34	Futo, Ito, Shizuoka Pref., Japan	2017	2018	FU	-	Seeds obtained from *P. edulis* (Carrière) Houz. 'Kikko-chiku'

[1]As *P. pubescens*.

[2]The year is not clear, but Y.Wakayama likely collected these seedlings during sporadic flowering in the moso bamboo forest at Wakayama Farm in 1968 (personal communication with T.Wakayama).

[3]See Kobayashi and Wakayama (2021).

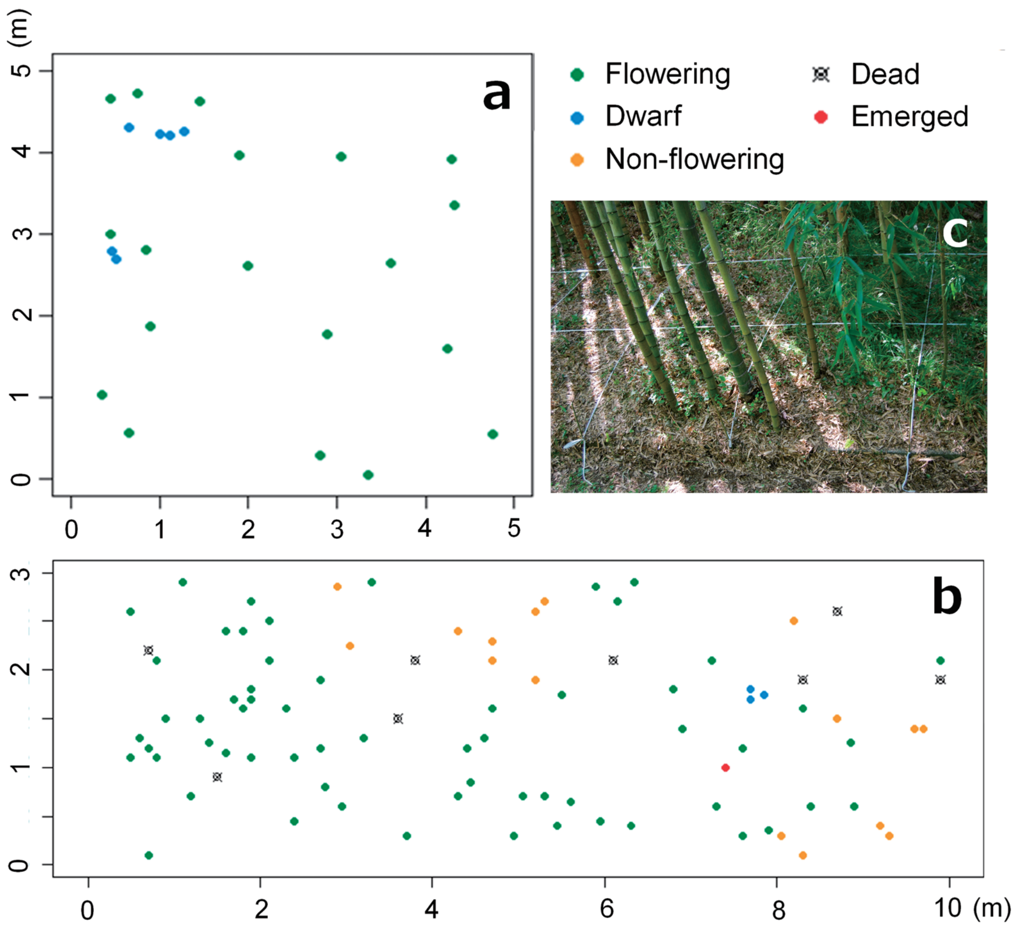

Fig. 2. Spacial distribution of all culms in both the Kamigamo Experimental Station (KA) (a) and the Fuji Bamboo Garden (FU) (b) in October 2021. c. Photo of the research plot at the FU site. Culms and shoots were categorized as flowering, non-flowering, dwarf, or dead. "*emerged*" denotes dwarf shoots that emerged after mass-flowering. Noted that at the FU site, one flowering culm was outside the plot.

both sites we have not yet confirmed the death of flowering culms, and the dynamics of non-flowering culms (Fig. 1h), flowering culms bearing leaves (Fig. 1i), and dwarf shoots (Fig. 1j–l) remain unassessed (Table 4, Fig. 2). These need to be investigated to clarify whether these stands are monocarpic in the strict sense.

Here, we reported a monocarpic life history of 66–69 years in some moso bamboo clones, while a single clone of this species, naturally occurring across Japan, has never mass-flowered since its introduction from China (Isagi et al. 2016, Kobayashi and Kobayashi 2019). This suggests that there is variation in life history traits, including reproductive characters, not only among species (Janzen 1976) but also within bamboo species. Mass flowering of bamboos follows an internal genetic clock, although some populations in the mass-flowering area sometimes do not flower for unknown reasons (Shibata 2010). Although the mechanisms and significance of such within-species variation will be the subject of future research, it has recently

Table 4. Summary of flowering status at the two study sites from July–October 2021 (see Table 1). Means ± standard deviations are shown. Dwarf shoots (Fig. 1j–l) were excluded from this summary.

Site code	Culm age	Flowering culms			Non-flowering culms		
		Number	Culm DBH (cm)	Culm height (m)	Number	Culm DBH (cm)	Culm height (m)
KA	1	0	–	–	0	–	–
	2	8	2.9 ± 0.6	4.1 ± 0.8	0	–	–
	≥ 3	11	4.0 ± 0.9	5.7 ± 1.4	0	–	–
	Total	19	3.6 ± 0.9	5.0 ± 1.4	0	–	–
FU	1	2	0.8 ± 0.1	2.8 ± 0.4	0	–	–
	2	3	3.4 ± 1.1	6.2 ± 1.6	1	7.8	ca. 15
	≥ 3	57	4.5 ± 1.9	7.7 ± 2.9	15	4.6 ± 2.7	9.0 ± 4.5
	Total	62	4.3 ± 2.0	7.5 ± 2.9	16	4.8 ± 2.7	9.4 ± 4.6

been suggested that not genetic factors but local environmental factors might be related to the within-species variation in life history patterns in the genus *Strobilanthes* Blume (*Acanthaceae*), which has three life histories: polycarpic perennial, monocarpic perennial, and periodical monocarpic (Kakishima et al. 2019). This finding might have implications for understanding the evolution of life history in bamboos.

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小林慧人[1,2]，西山典秀[3]，柏木治次[4,5]，柴田昌三[6]：**モウソウチク（イネ科）が半世紀以上の栄養成長期を経て一斉開花した**

タケ（イネ科）は長寿命の一回繁殖性を示す植物であると知られるが，実生から有性生殖までを評価できた研究はほとんどない．2021 年 7 月，京都大学上賀茂試験地（京都府）と富士竹類植物園（静岡県）で実生の段階より保育されてきたモウソウチク *Phyllostachys edulis* (Carrière) J.Houz. [= *P. pubescens* (Pradelle) J.Houz., *P. heterocycla* (Carrière) Matsum. var. *pubescens* (J.Houz.) Ohwi] の林が一斉開花の様相を示した．筆者らはこの珍しい開花現象を観察し，過去の栽培記録や両施設のスタッフらへのインタビューに基づき，開花時の林齢がそれぞれ 66 年，67 年であると推定した．先行研究と合わせて考えると，日本国内には 66–69 年の寿命で一回繁殖性を示すモウソウチクがあることがわかった．一方，現在日本各地に生育するモウソウチク林はおよそ単一クローンと考えられており，中国より導入後およそ 300 年が経過する中で未だ一度も一斉開花していない．これらから，モウソウチクの繁殖特性などの生活史の様式には，種内変異があることが示唆された．

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