Title:

CHARACTERISTICS OF A FLOWERING EVENT OF ARROW BAMBOO, Fargesia qinlingensis

Authors:

Wei Wang\textsuperscript{a},
\textsuperscript{a}Strategic & Analytic Consulting Group, Epsilon, 4445 Lake Forest Drive, Suite 200, Blue Ash, OH 45242, E-mail: wwang@epsilon.com

Scott B. Franklin\textsuperscript{b,*},
\textsuperscript{b}Author of correspondence, \textsuperscript{a}School of Biological Sciences, University of Northern Colorado, Greeley, CO 80639, USA; Ph. (970) 351-2650, Fax (970) 351-2335, E-mail: scott.franklin@unco.edu

Zhijun Lu\textsuperscript{c},
\textsuperscript{c}Key Laboratory of Aquatic Botany and Watershed Ecology, Chinese Academy of Sciences Wuhan 430074, P.R. China; luzj@wbgcas.cn

and Brian J. Rude\textsuperscript{d}
\textsuperscript{d}H. W. Essig Nutrition Lab, Mississippi State University, Mississippi State, MS 39762, USA; E-mail: brude@ads.msstate.edu

Running head: Characteristics of a bamboo flowering event
CHARACTERISTICS OF A FLOWERING EVENT OF AN ARROW BAMBOO
FARGESIA QINLINGENSIS

Abstract. The characteristics of flowering sites and un-flowered patches of an arrow bamboo (Fargesia qinlingensis) were studied and compared at a watershed in Qinling Mountains, China, over a three-year period (2003, 2004, and 2005) after a mast flowering event. Density of live culms decreased over the three years in both flowering sites and un-flowered patches. New shoots regenerated only in un-flowered patches. Basal diameter and height of culms displayed no significant differences between flowering sites and un-flowered patches. Seedling density was significantly greater in flowering sites than in un-flowered patches, and was greater in 2004 than in 2005. Seedlings performed better in flowering sites than in un-flowered patches based on their height, leaf number per seedling, and average leaf length in one study site. Seedling mortality rate was greater in un-flowered patches than in flowering sites. Chemical constituent allocation varied among culm parts (stems, branches, and leaves), with leaves containing more crude protein, hemi-cellulose, and extract ether (crude fat) and less organic matter, neutral detergent fiber (hemi-cellulose, cellulose and lignin), and acid detergent fiber (cellulose and lignin) compared to branches and stems. Crude protein and extract ether in branches and leaves were less in flowering culms than in un-flowered culms. Aboveground biomass of culms in un-flowered patches was three orders of magnitude greater than that of seedlings in flowering sites. This study suggested that the characteristics of bamboos and bamboo stands were dramatically altered during this flowering event in terms of seedling establishment and chemical constituent allocation.

Key Words: Qinling Mountains; semelparity; flowering; energy allocation; biomass; seedlings.
INTRODUCTION

Several bamboos are semelparous, having an unusual life history including a long clonal phase (sometimes over 100 years), followed by mass synchronous flowering and subsequent death (Janzen, 1976; Tian, 1987; Qin et al., 1989; Taylor et al., 1991). The long inter-mast period has inhibited documentation of stand changes (Marchesini et al. 2009; Abe & Sibata 2012; Austin & Marchesini 2012) and a thorough understanding of bamboo regeneration, because flowering events are relatively rare (but see Kakishima et al. 2012 and de Carvalho et al. 2013). Further, the evolutionary selection for semelparity in bamboos is still debated (Keeley & Bond 1999; Saha & Howe 2001; Franklin 2004; Sadananda et al. 2010; Iler & Inouye 2013). Our interest is with the habitat bamboo forests provide throughout the world (Franklin 2004; Nath & Das 2010; Dar et al. 2012), and specifically for giant panda and other endangered species in the Qinling Mountains of China (Tian 1988). Semelparous die-off events result in the loss of habitat for several years. In this study, we examined changes of stand structure, culm characteristics, and energy allocation in Fargesia qinlingensis Yi et Shao during a flowering event in order to: (1) document energy allocation during flowering, (2) document regeneration following die-offs, and (3) add anecdotal evidence toward our understanding of selection for semelparity. Our goal is to better understand the biology of gregarious-flowering, semelparous long-lived bamboos, and subsequently manage for major modifications following die-offs in habitat of endangered species.

For some bamboo species, restoration of bamboo forest relies exclusively on regeneration from seeds after flowers and dies, because rhizomes die after culms flower (Tian, 1987; Keeley and Bond 1999.). Biotic (birds, mammals, insects, etc.) and abiotic (light, water, nutrients, etc.) factors affect seed production and seedling establishment, making the early life-stage of plants vulnerable (Grubb, 1977; Harper, 1977; Grime, 1979). Bamboo seed germination and seedling establishment and growth may be affected by bamboo die-off due to the change of light, temperature, and nutrients, such as in temperate forests dominated by Sasa kurilensis in Japan (Abe et al. 2001, 2002) and by B. fangiana in China (Taylor and Qin, 1988). Indeed, such resource change is at the heart of the intraspecific competition hypothesis (Janzen, 1976; Gadgil and Prasad, 1984; Taylor et al., 1991; Franklin and Bowman, 2003), which explains the long clonal phase of semelparous bamboos as habitat modification. Stearns’ (1980) habitat modification theory suggests semelparity is selected for when adult longevity changes environmental conditions such that successful seedling recruitment is increased. Bamboo expands vegetatively over a long period of time sequestering a large spatial patch, then flowers and dies, leaving ample resources and little competition in its wake for seedlings to germinate and grow.

Seed distribution may also be affected by seed predators due to rodent outbreaks following bamboo flowering (Jaksic and Lima 2003), the so-called predator satiation hypothesis of semelparity (Janzen, 1976; Gadgil and Prasad, 1984). But seed and seedling predation pressure is different in flowering areas and non-flowering areas. For example, seed and seedling predations are reduced in die-off areas compared to non-die-off areas of Sasa kurilensis (Abe et al. 2001, 2002). Thus, a higher seedling establishment may be expected in flowering areas. Kakishima et al. (2011) found evidence for selection of gregarious flowering of Strobilanthes flexicaulis by pollinator activity and predator satiation. An argument against the predator satiation hypothesis is no clear selection force that would result in such long periods of clonal growth (Keeley and Bond, 1999).
Flowering of bamboo may influence the energy allocation in bamboo modules. Some plants sacrifice growth for the sake of reproduction (Abrahamson and Caswell, 1982). The energy allocated to reproduction gradually increases as buds become flowers, flowers are fertilized and seeds mature (Harper and Ogden, 1970). Lupine (*Lupinus nanus* ssp. *latifolius* (Benth.) D. Dunn.) distributes up to 61% of its energy to reproductive tissues and 29% to seeds (Pitelka, 1977). The increase of energy to reproductive organs may hence decrease energy allocated to vegetative organs, and is the heart of the resource hypothesis of semelparity (Gadgil and Bossert, 1970; Schaffer, 1974), which suggests that a period of time is needed to acquire the necessary resources for flowering, and that the resources are exhausted during the flowering event. Little has been done on changes in resources and chemistry with flowering bamboo. However, it is reasonable to predict that they may allocate a large proportion of energy to reproduction because bamboos die after flowering.

The flowering of an arrow bamboo *F. qinlingensis*, one of giant panda’s main food resource in the Qinling Mountains, offers a rare opportunity to compare stand characteristics in unflowered patches and adjacent flowering areas. Such comparisons provide a novel approach to studying bamboo flowering and subsequent regeneration. We monitored the flowering event for five years, including an analysis of energy availability in flowered and unflowered culms to elucidate exhaustion of resources, and developed a nutrient addition study to examine habitat modification. The objectives of this study were to: (1) compare growth characteristics of culms in flowering sites and unflowered sites, (2) compare seed production and seedling establishment in flowering sites and unflowered sites, (3) compare biomass differences between culms in unflowered sites and seedlings in flowering sites, (4) compare seedling growth following nutrient supplement treatments in flowered and unflowered patches, and (5) compare energy allocation in flowering culms and unflowered culms. We also discuss anecdotal evidence regarding selection for semelparity in bamboo.

**METHODS**

**Study area**

This study was carried out at the Taibaishan National Natural Reserve (TNNR, 33° 49´ 30´´ - 34° 05´ 35´´ N, 107° 22´ 25´´ - 107° 51´ 30´´ E) in Qinling Mountains, Shaanxi Province, China. TNNR is in the southern end of the warm temperate zone with four distinguished seasons. It is the northern range of giant panda’s distribution. Mean annual temperature is 8.4°C; -4.2°C in January and 20.4°C in July. Precipitation averages 945.5 mm/year with 50% falling between July and September. The soil in the flowering area is rhogosol brown soil (pH 6.2) that forms from granite. The lower part of the soil is semi-weathered parent material with pH 6.5.

Vegetation is diverse due to the coexistence of both northern and southern Chinese taxa. Forest communities cover 81% of TNNR, made up of four general vegetation types along an elevation gradient: oak forests (1500-2000 m), birch forests (2000-2500 m), coniferous forests (2500-3540 m), and alpine shrublands and meadows (3450-3700 m). Two main bamboo species are distributed in Qinling Mountains; *F. qinlingensis* predominates at higher elevations (1700-3000 m) and *Bashania fargesii* (Camus) Keng et Yi at lower elevations (900-1900m).

**Study species**
*F. qinlingensis* has a pachymorph rhizome (Li et al., 2003), and its culm can grow up to 3.6 m in height and 13 mm in basal diameter. New shoots regenerate from rhizomes in May and June.

During the flowering period, it flowers in April and sets seed in June. Like most other bamboos in tropical and temperate regions (Janzen, 1976; Gadgil and Prasada, 1984), *F. qinlingensis* is also a perennial monocarpic species which is known for its long period of vegetative growth followed by a mast seeding; it has a seeding cycle of ca. 50 years (Tian, 1987). In TNNR, sporadic flowering of *F. qinlingensis* began in 1999 in a watershed and mast flowered throughout this watershed in an area of ca. 300 ha from 2001 to 2003 (Yue and Li personal communication). The temporal gregarious flowering with a few early, a few late, and most flowering during one year has been documented in other bamboo species (Abe & Shibata 2012; de Carvalho et al. 2013). A small amount of un-flowered patches of mature culms grew within a matrix of dead and flowering culms, as has been observed in other studies (Marchesini et al. 2009). The un-flowering areas had the approximate shape of an ellipse. Similar mosaic patterns of live and dead culms have been reported for other bamboos, such as *B. fangiana* in Qionglai Mountain, Sichuan Province, China (Schaller et al., 1985; Taylor and Qin, 1987; Johnson et al., 1988; Taylor and Qin, 1988; Reid et al., 1989; Taylor et al., 1991).

### Field methods

Three sites with un-flowered patches were randomly selected for study. The length and width of each patch was measured, and area calculated by using an elliptical formula. The areas of the three un-flowered patches were 240.33, 66.76, and 159.06 m², respectively. The three sites had similar topographic characteristics, canopy cover, and bamboo cover (Table 1). Herb cover was greatest in site 1. All three sites were in a broad-leaved forest mixed with a very small proportion of conifers. There were obvious layers of canopy, sub-canopy, and understory. Dominant canopy species consisted of *Quercus spinosa* David, *Quercus aliena* Bl var. *acuteserrata* Maxim, and *Juglans cathayensis* Dode etc. Species in the shrub layer mainly included *Morus alba* Linn, *Lespedeza bicolor* Turcz, and *Smilax riparia* A. DC. *F. qinlingensis* dominated the understory of the forest.

Six 1 × 1 m plots were randomly set up in each of the three un-flowered patches. Another six 1 × 1 m plots were randomly set up in each flowering area near the un-flowered patch. In each 1 × 1 m plot, basal diameter of each ramet was measured to its nearest 0.01mm in October 2003, and re-measured over the next four years (2003-2007). Ramets were divided into four categories: new shoots, flowering culms, live culms, and dead culms. New shoot (< 1 year old) and culms (> 1 year old) specifically refer to vegetative reproduction, not seedling.

Total seedlings of *F. qinlingensis* were counted in each 1 × 1 m plot from 2004 to 2007. No seedlings were established in 2003. In 2004, ten randomly selected seedlings, or all seedlings if there were less than 10 seedlings in the 1 × 1 m plot, were measured for height and leaf length to the nearest 0.1 cm. In June 2005, measurements were repeated for 1-year-old and two-year-old seedlings.

Twenty flowering culms were randomly selected from each of the three flowering sites in October 2003. Florets and actual seeds on each culm were counted. In addition, five 0.5 × 0.5 m plots were randomly set up in each flowering site. Soil of 10 cm deep in each plot was extracted and all viable seeds (with white color embryo) were counted. We also randomly selected and
marked 10 culms that started to flower in 2003 in each flowering site. They were revisited in August 2004 and June 2005 to determine survival.

In October 2003, ten flowering culms from each flowering site and un-flowered patch were randomly collected and sorted by culm parts (stems, branches, and leaves), and then were dried for analysis. Culms were randomly split into two groups to garner enough material for all analyses. Chemical constituents in each culm part were analyzed at Mississippi State University, providing dry matter percentage of organic matter (OM), crude protein (CP), neutral detergent fiber (NDF; lignin, cellulose, and hemi-cellulose), acid detergent fiber (ADF; lignin and cellulose), hemi-cellulose (HC = NDF - ADF), and extract ether (EE; crude fat).

In the fall of 2006, we applied nitrogen and phosphate addition as two factors and randomized block design with four treatments: +N, +P, N+P and no fertilizer addition within six blocks (three blocks in the flowering zone and three blocks in the non-flowering zone), 24 plots at each site, for a total of 72 plots at three sites. This research examines one aspect of the habitat modification hypothesis for semelparity: is adult death (which results in increased light and nutrients to the area) necessary for long-term seedling survival. Measurements of bamboo seedlings (taken 1 yr later in 2007) included density, height, number of branches, number of leaves, and the length of the three longest leaves (subsequently averaged). We calculated plot averages of each growth variable prior to running analyses.

**DATA ANALYSIS**

**Density and characteristics**

We used a mixed linear model to analyze the data with repeated measures in a randomized complete block design with six replications in each experimental unit (1 x 1 m plot) to test the flowering effect (two levels: flowering site and un-flowered patch) and time effect (five levels: 2003, 2004, 2005, 2006 and 2007) on the density of live culms in the flowering sites and the un-flowered patches. Flowering and time were considered fixed effects and block and interaction of block and flowering were considered random effects. If there was a significant interaction between the flowering effect and time effect, a multiple comparison with Bonferroni adjustments was performed to seek significant differences among the treatment combinations. These analyses were performed by using the MIXED procedure in SAS (SAS Institute, 2004).

Density of total seedlings and seedlings established in 2004 in flowering sites and un-flowered patches were tested using two mixed linear models as described for culms. In addition, a two-way multivariate analysis of variance (MANOVA) was performed to examine differences in seedling variables (height, average leaf length, and leaf number per seedling) in relation to flowering and age in site 3 (site 1 and site 2 were excluded from this analysis because of the low number of seedlings in un-flowered patches in these two sites). Each seedling was considered a replicate. The two main effects were flowering (two levels: flowering site and un-flowered patch) and age (two levels: 1-year old and 2-years old). Main effects were considered fixed. Three protected two-way ANOVAs were performed to test the effect of flowering and age on each dependent variable. A multiple comparison with Bonferroni adjustment was performed to seek significant differences among four treatment combinations (1-year-old/flowering site; 1-year-old/un-flowered patch; 2-years-old/flowering site; 2-years-old/un-flowered patch) if there was a significant interaction between flowering and age. Analyses were performed by using the GLM procedure in SAS (SAS Institute, 2004).
For the fertilization experiment, a two-factor ANOVA (flowering and nutrients) examined the differential effects of fertilization in flowering and un-flowering areas using the GLM procedure in SAS (SAS Institute, 2004). Data were log-transformed for normality prior to analysis.

Chemical constituents’ allocation in culms

A randomized complete block design with two replications in each experimental unit (bamboo culm) was analyzed by using the MIXED procedure in SAS/STAT (SAS Institute 2004) to test for flowering effect (two levels: flowering site and un-flowered patch) and culm part effect (three levels: leaf, branch, and culm) on the six chemical constituent variables (OM%, CP%, NDF%, ADF%, HC%, and EE%). Two main effects (flowering and culm part) were considered fixed, and block effect was considered random. If there was a significant interaction between the two main effects, a multiple comparison with Bonferroni adjustments was performed to seek significant differences among six treatment combinations (flowering/stem; flowering/leaf; flowering/branch; un-flowered/stem; un-flowered/leaf; un-flowered/branch) for each dependent variable. These analyses were performed by using the MIXED procedure in SAS (SAS Institute, 2004). Percentage data were arcsin square root transformed prior to analysis to meet the assumptions of normality and homogeneity of variances. For all analyses, differences were considered significant at P < 0.05 level.

RESULTS

Density and characteristics of culms

No new shoots regenerated from rhizomes in the flowering sites during the three studied years. However, new shoot regeneration occurred every year in the three un-flowered patches except site 2 in 2005 (Fig. 1). There was a significant effect of flowering and time interaction on the density of live culms ($F_{2, 98} = 3.55, P = 0.0324$). Density decreased dramatically in the flowering site over the three years (Fig. 2a). Surprisingly, density of live culms in un-flowered patches also significantly decreased over the three years (Fig. 2a). The density of live culms in un-flowered patches was significantly greater than that in flowering sites every year (Fig. 2a). Four of 30 culms that started to flower in 2003 died in 2004, half of them (15 culms) were still alive in 2005, but none remained in 2006.

Seed density and seedling establishment

In the three flowering sites, average floret density ($2687 \pm 847$ florets/m$^2$) was much greater than average density of actual seeds on culms ($53 \pm 20$ seeds/m$^2$) and seeds in soil seed bank ($5 \pm 2$ seeds/m$^2$). Density of 1-year-old seedlings averaged $27 \pm 2$ seedlings/m$^2$ (Table 2).

Density and characteristics of seedlings

No seedlings were established until 2004. We found no significant effect of time and flowering interaction on either density of total seedlings or density of seedlings established in 2004 (Table
However, Densities of total seedlings and seedlings established in 2004 were significantly greater in flowering sites than in un-flowered patches (Table 3; Fig. 3a, c), and were significantly greater in 2004 than in 2005 (Table 3; Fig. 3b, d). 39.0% of seedlings that established in flowering areas in 2004 survived until 2005, and 16.9% of seedlings established in un-flowered patches in 2004 survived until 2005.

We found a significant interaction between flowering and age on seedling height; two-year old seedlings were significantly taller in flowering areas than un-flowered areas (Table 4, Fig. 3a). Both flowering and age significantly affected number of leaves and average length of leaves (Table 4). Two-year-old seedlings had significantly more leaves (Table 4, Fig. 4b) and longer leaf lengths (Table 4, Fig. 4c) than did one-year-old seedlings. Leaf length was significantly longer in flowering sites than in un-flowered patches (Table 4, Fig. 4d).

Chemical constituents’ allocation

The interaction of flowering and culm part type was significant for all six chemical compounds (Table 5). OM% was significantly greater in flowering branches than in un-flowered branches (Fig. 5a). Leaves contained much more CP% than branches and stems (16.1% and 13.0% compared to 5.4% and 4.2% in branch and 1.5% and 1.6% in stem for un-flowered culms and flowering culms, respectively), and CP% in leaves and branches was significantly greater for un-flowered culms than for flowering culms (Fig. 5b). Two less-digestible fiber constituents (NDF% and ADF%) had the same trend: stems > branches > leaves. Fibers’ percentages in stems were significantly greater for un-flowered culms than flowering culms, but the differences were not significant for branches and leaves (Fig. 5c, d). Hemi-cellulose (HC%) was significantly different among culm parts: leaves > branches > stems, but there was no significant difference between flowering culms and un-flowered culms (Fig. 5e). Leaves contained more crude fat (EE%) than branches and stems for un-flowered culms (13.9% compared to 12.5% and 10.4% in branches and stems), and crude fat in leaves and branches was significantly greater for un-flowered culms than flowering culms (Fig. 5f).

Two rhizomes from a flowering site and an adjacent un-flowered patch were analyzed, and seeds from several flowering culms were also analyzed, rendering only enough material for one set of chemical constituent analyses each (n=1). Greater amount of easily digestible crude fat and partially digestible hemi-cellulose were found in seeds compared to all other culm parts (Fig. 5f, g). Chemical amounts in rhizomes were similar to branches and stems. Little difference was found between the flowered and un-flowered rhizome samples, but flowered rhizomes generally had less chemical levels.

Nutrient Supplement

DISCUSSION

Our results show that flowering of *F. qinlingensis* has significantly altered stand characteristics. Live culms dramatically declined in flowering areas from 2003 to 2005, and only a small amount of flowering culms remained in 2005. Surprisingly, live culms also decreased over the three-year period in the un-flowered patches, suggesting a negative effect of flowering on the un-flowered patch. One probable reason may be that some culms generate from rhizomes running from
flowering areas. Other explanations may include the changed environments after culms die, such as the increased light under dead bamboo canopy (Taylor and Qin (1988), temperature fluctuations (Abe et al. 2001, 2002), and predator outbreaks (Jaksic and Lima 2003).

Half of the flowering culms of *F. qinlingensis* survived for at least two years. A similar phenomenon has been reported for individuals of *Fargesia robusta* Yi that can live for 2 to 3 years after flowering in Min Mountains (Qin et al., 1993). New shoots stopped generating in flowering sites, while in the nearby un-flowered patches, new shoots continued to regenerate every year. The reason why vegetative reproduction stopped when the sexual reproduction started is probably because of the reallocation of energy from culms to reproduction organs. It has been reported that some plants sacrifice growth for the sake of reproduction (Abrahamson and Caswell, 1982). The energy allocated to reproduction gradually increases as buds become flowers, flowers are fertilized and seeds mature (Harper and Ogden, 1970). The increase of energy to reproductive organs may hence decrease energy allocated to vegetative organs. Our data, however, suggests that all energy was not exhausted, and that there were not extreme differences between flowered and un-flowered culms, both points arguing against the resource allocation hypothesis.

Although the flowering started from 1999, no seedlings were established until 2004, suggesting delayed germination. Seeds of *B. fangiana* are reported to remain dormant for at least two years in Qionglai Mountains (Taylor and Qin, 1988). Qin (1985) also reports that seeds of *F. scabrida* remain dormant in the soil up to five years in Min Mountains. Recent work on *Chusquea* also identify multi-year dormancy (González et al. 2002). Dormancy would suggest against the predator satiation hypothesis for semelparity, as it would only lead to higher predation rates. However, seeds of *F. qinlingensis* showed no dormancy characteristics in the lab, germinating any time of year under both light and dark conditions (W. W. et al. Unpublished data).

The number of seeds in the soil seed bank and in the culms was much less than the florets, suggesting that a large portion of seeds had been removed or eaten. Although most bamboos set large quantities of seeds (Janzen, 1976), seeds are preyed upon heavily by invertebrates (e.g. insects, Taylor and Qin, 1988; Zheng, 1994) and vertebrates (e.g. rodents and birds, Janzen 1976). It has been hypothesized that the adaptive significance of mast seeding is to swamp predators, the predator satiation hypothesis (Janzen, 1976; Gadgil and Prasad, 1984; Keeley and Bond, 1999). Therefore, our data on seed numbers may underestimate fecundity of *F. qinlingensis* because rodent outbreaks often follow bamboo flowering (Jaksic and Lima 2003). While number of florets may be a better indicator, there is no way of knowing how many viable seeds were developed.

Densities of *F. qinlingensis* seedlings in flowering site (28 ± 2 seedlings/m² and 19 ± 2 seedlings/m² in 2004 and 2005, respectively) are less than that reported by Tian (1987). In his study, the density of *F. qinlingensis* is as high as 405 seedlings/m². Densities of seedlings is also less than that of two populations of *Chusquea tomentosa* Widmer & Clark reported by Stern et al. (1999) in Costa Rica (54 seedlings/m² and 38 seedlings/m²) and *B. fangiana* in Sichuna of China (up to 97 seedlings/m²) (Taylor and Qin, 1988). The low establishment rate of *F. qinlingensis* was probably because of low seed density in the soil seed bank, or due to the suppression of seed germination and root elongation by moss and litter, which is the case for *B. fangiana* (Zhou and Huang, 1996). High predation may be also contributed to low seedling establishment. A relatively low number of established seedlings are also noted in another bamboo, *Melocanna baccifera* (Roxburgh) Kurtz ex Skeels in Sri Lanka, due to many fruits.
being devoid of an embryo (Ramanayake and Weerawardene, 2003). Survival rate of *F. qinlingensis* (39% and 17% in flowering site and un-flowered patch, respectively) in this study is lower than that of *B. fangiana* (62-85%) in Sichuan, China (Taylor and Qin, 1988).

Seedlings grew slow in this study. Two-year-old seedlings had heights of 7.97 cm and 6.01 cm in flowering sites and un-flowered patches, respectively. Slow growth also is noted for *C. tomentosa* (Stern et al., 1999). Qin et al. (1989) report that three-year-old seedlings of *B. fangiana* averaged only 6.7 cm high. Reid et al. (1989) report that *B. fangiana* four-year-old seedlings are no more than 10-15 cm tall. Researchers have estimated the time for bamboo seedlings to grow back to their original full size after a flowering event: 19 years for *F. qinlingensis* in Qinling Mountains, Shaanxi, China (Tian, 1991); 15 to 20 years for *B. fangiana* and *F. scabrida* in Qionglai Mountains, Sichuan, China (Qin et al., 1989; Taylor and Qin, 1993); and 16 to 19 years for *F. denudata* in Min Mountains, Gansu, China (Huang, 1994). Data comparing *F. qinlingensis* areas that flowered in the early 1980s versus adjacent un-flowered areas (W. W. et al. unpublished data) show little difference in density or culm diameter, suggesting recovery occurs within 20 years following flowering in the Qinling Mountains.

Seedlings performed better in flowering sites than in un-flowered patches. The better growth and greater survival rates of seedlings in flowering sites than in un-flowered patches probably resulted from the resource change caused by death of culms (Abe et al. 2001, 2002; Taylor and Qin 1988). Greater light levels and reduction of mineral nutrient uptake from soils with bamboo rhizome death results in increased resources that could be used by bamboo seedlings in flowering sites (Taylor and Qin, 1988). The better performance of seedlings in flowering sites may support the intraspecific competition hypothesis for mast seeding of bamboos (Janzen, 1976; Gadgil and Prasad, 1984; Taylor et al., 1991; Franklin and Bowman, 2003). Few plants establish and survive beneath dense culms because most resources for plant growth are used by established culms. Mast seeding followed by die-off of mature clones would permit offspring to regenerate without parental competition for resources (Taylor et al., 1991).

Chemical constituents’ allocation in different culm parts of *F. qinlingensis* were similar to other bamboos consumed by giant pandas. Leaves of both flowering culms and un-flowered culms contained more crude protein than branches and stems. Similar results are reported in *Phyllostachys aureosulcata* McClure by Dierenfeld et al. (1982) and in *B. fangiana* by Qin et al. (1993). But CP% in leaves of these three bamboos is slightly different: *B. fangiana* (19.44%) > *F. qinlingensis* (16.1%, this study) > *P. aureosulcata* (13%). Two fibers’ (NDF and ADF) allocation in *F. qinlingensis* had the same trend: stems > branches > leaves, matching that of *F. scabrida* (Schaller et al., 1990). Organic matter and hemi-cellulose also have the same trend (leaves > branches > stems) as *F. scabrida* (Schaller et al., 1990). Leaves of un-flowered culms had more crude fat than stems and branches, which is similar to *B. fangiana* (Qin et al., 1993), but crude fat content is much greater in *F. qinlingensis* (10.4%, 12.5%, and 13.9% in stems, branches, and leaves, respectively) than in *B. fangiana* (0.59%, 2.4%, and 3.4% in stems, branches, and leaves, respectively).

Organic matter in branches was greater in flowering culms than in un-flowered culms, while less-digestible fibers (NDF and ADF) in stems were greater in un-flowered culms than in flowering culms. Crude protein and crude fat in leaves and branches were greater in un-flowered culms than in flowering culms. One explanation is that the allocation of energy to reproduction increased energy allocated to vegetative organs (Leopold and Kriedemann, 1975). Crude fat had the greatest concentration in seeds, and both crude fat and crude protein were significantly less in branches and leaves of flowering plants. If crude fat was moved from the branches and leaves to...
fruit production, a dilution effect would be seen with increases in the percentage of non-
digestible chemicals in other culm parts. Such an increase was only found in organic matter.

In conclusion, our results suggested that the characteristics of bamboos and bamboo stands
were dramatically altered during this flowering event in terms of culm dynamics, seedling
establishment, and chemical constituent allocation. We have shown evidence that allocation of
energy toward growth is sacrificed for allocation toward flowering and fruiting, but the amount
does not appear dramatic enough to support an exhaustion of resources. Our data support other
studies suggesting slow seedling growth, enhanced growth in areas without a bamboo canopy,
and a long regeneration time for bamboo stands, supporting the habitat modification hypothesis
for semelparity. We have conflicting results regarding the predator satiation hypothesis.
Dormancy would seem to argue against such a hypothesis, while the low number of regenerating
individuals compared to the number of potential seeds from counted empty florets, and their
being distributed into un-flowered areas, suggests predation was a factor. While we have no data
on seed herbivory, we agree with Keeley and Bond (1999) that suggest extended periods of time
in between flowering (c. 50 years for F. qinlingensis) seems too long for the sole purpose of off-
setting herbivore populations.

ACKNOWLEDGEMENTS

We would like to thank J. Li, the director of the Houzhenzi Protection Station of TNNR for
allowing us to conduct this research in the reserve and for his arrangement and help in the field.
We would also like to thank Z. Lu, L. Zhao, X. Du, H. Li, and T. Yue for their assistances in the
field. This research was supported by the Memphis Zoo.

REFERENCES

Abe M., Miguchi H., and Nakashizuka T. 2001. An interactive effect of simultaneous death of
dwarf bamboo, canopy gap, and predatory rodents on beech regeneration. Oecologia,
127: 281-286.
Sasa and canopy gap formation on tree regeneration in an old beech forest. Journal of
Vegetation Science 13: 565-574.
Abrahamson, W.G., Caswell, H., 1982. On the comparative allocation of biomass energy, and
nutrients in plants. Ecology 63, 982-991.
arunhema (Bambuseae: Poaceae) after mass-flowering and die-off at contrasting sites in
Franklin, D.C., 2004. Synchrony and asynchrony: observations and hypotheses for the flowering
wave in a long-lived semelparous bamboo. J. Biogeogr. 31, 773-786.
lowland Nothofagus-dominated forest after bamboo dieback in South-Central Chile. Plant


Table 1. The characteristics of three un-flowered patches of *Fargesia qinlingensis* at the Taibaishan National Natural Reserve, Shaanxi Province, China.

<table>
<thead>
<tr>
<th>Patch</th>
<th>Area (m²)</th>
<th>Slope steepness (°)</th>
<th>Slope aspect (°)</th>
<th>Elevation (m)</th>
<th>Canopy cover (%)</th>
<th>Canopy height (m)</th>
<th>Herb cover (%)</th>
<th>Bamboo cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>240.33</td>
<td>26</td>
<td>234</td>
<td>1850</td>
<td>85</td>
<td>18</td>
<td>70</td>
<td>75</td>
</tr>
<tr>
<td>2</td>
<td>66.76</td>
<td>18</td>
<td>162</td>
<td>1910</td>
<td>80</td>
<td>18</td>
<td>70</td>
<td>70</td>
</tr>
<tr>
<td>3</td>
<td>159.06</td>
<td>30</td>
<td>180</td>
<td>1880</td>
<td>70</td>
<td>17</td>
<td>25</td>
<td>60</td>
</tr>
</tbody>
</table>
Table 2. Flower and seed characteristics of *Fargesia qinlingensis* from three flowering sites in the Taibaishan National Natural Reserve, Shaanxi Province, China, in October 2003.

<table>
<thead>
<tr>
<th>Site</th>
<th>Total florets /culm (1 SE)</th>
<th>Actual seeds/culm (1SE)</th>
<th>Florets/m² (1SE)</th>
<th>Actual seeds on culms/m² (1 SE)</th>
<th>Seeds in soil/m² (1 SE)</th>
<th>Seedlings/m² (1 SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>183.5 (30.4)</td>
<td>3.8 (1.5)</td>
<td>3303 (843.6)</td>
<td>68.4 (17.5)</td>
<td>8.8 (2.9)</td>
<td>29.8 (5.2)</td>
</tr>
<tr>
<td>2</td>
<td>299.6 (39.9)</td>
<td>6.2 (1.6)</td>
<td>3745 (253.6)</td>
<td>77.5 (5.25)</td>
<td>5.2 (2.3)</td>
<td>28.7 (13.2)</td>
</tr>
<tr>
<td>3</td>
<td>242.9 (44.9)</td>
<td>3.0 (0.8)</td>
<td>1012.1 (211.9)</td>
<td>12.5 (2.6)</td>
<td>1.8 (0.8)</td>
<td>23.6 (9.6)</td>
</tr>
<tr>
<td>Average</td>
<td>242.0 (33.5)</td>
<td>4.3 (1.0)</td>
<td>2686.7 (847.0)</td>
<td>52.8 (20.3)</td>
<td>5.3 (2.0)</td>
<td>27.4 (1.9)</td>
</tr>
</tbody>
</table>
Table 3. Summary of analysis of density of total seedlings and density of seedlings of *Fargesia qinlingensis* established in 2004 at the Taibaishan National Natural Reserve, Shaanxi Province, China. Variable flowering had two levels: flowering sites and un-flowered patches. Variable time had two levels: years 2004 and 2005.

<table>
<thead>
<tr>
<th>Fixed Effects</th>
<th>Total seedling</th>
<th>Seedling established in 2004</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>F</em></td>
<td><em>P</em></td>
</tr>
<tr>
<td>Flowering (F)</td>
<td><em>F</em>1,2 = 27.68</td>
<td>0.0343</td>
</tr>
<tr>
<td>Time (T)</td>
<td><em>F</em>1,64 = 7.44</td>
<td>0.0082</td>
</tr>
<tr>
<td>T × F</td>
<td><em>F</em>1,64 = 0.20</td>
<td>0.2833</td>
</tr>
</tbody>
</table>
Table 4. Summary of analysis of seedling height, average leaf length, and number of leaves per seedling of *Fargesia qinlingensis* in site 3 at the Taibaishan National Natural Reserve, Shaanxi Province, China. Variable flowering had two levels: flowering site and un-flowered patch. Variable age had two levels: 1-year-old and 2-year-old seedlings.

<table>
<thead>
<tr>
<th>Effect</th>
<th>MANOVA</th>
<th>Height</th>
<th>Number of leaves</th>
<th>Length of leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$F_{3,129}$</td>
<td>$P$</td>
<td>$F_{1,131}$</td>
<td>$P$</td>
</tr>
<tr>
<td>Flowering (F)</td>
<td>2.90</td>
<td>0.0376</td>
<td>3.43</td>
<td>0.0664</td>
</tr>
<tr>
<td>Age (A)</td>
<td>11.04</td>
<td>0.0001</td>
<td>32.33</td>
<td>0.0001</td>
</tr>
<tr>
<td>F × A</td>
<td>1.85</td>
<td>0.1414</td>
<td>4.40</td>
<td>0.0378</td>
</tr>
</tbody>
</table>
Table 5. Summary of six mixed linear models for chemical compound variable of *Fargesia qinlingensis* collected from the Taibaishan National Natural Reserve, Shaanxi Province, China. OM = organic matter, CP = crude protein, NDF = neutral detergent fiber (ligning, cellulose, and hemi-cellulose), ADF = acid detergent fiber (ADF; lignin and cellulose), HC = hemi-cellulose (HC=NDF-ADF), and EE = extract ether (crude fat). Variable Flowering had two levels: flowered site and un-flowered site. Variable Part had three levels: leaf, branch, and culm.

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>OM%</th>
<th>CP%</th>
<th>NDF%</th>
<th>ADF%</th>
<th>HC%</th>
<th>EE%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flowering (F)</td>
<td>6.44 (1,2)</td>
<td>15.04 (1,2)</td>
<td>2.96 (1,2)</td>
<td>0.47 (1,2)</td>
<td>0.00 (1,2)</td>
<td>23.28 (1,2)*</td>
</tr>
<tr>
<td>Part (P)</td>
<td>37.32 (2,26) ***</td>
<td>1178.81 (2,26) ***</td>
<td>670.52 (2,26) ***</td>
<td>1019.37 (2,26) ***</td>
<td>346.81 (2,26) ***</td>
<td>48.53 (2,26) ***</td>
</tr>
<tr>
<td>F × P</td>
<td>3.64 (2,26) *</td>
<td>9.11 (2,26) **</td>
<td>28.04 (2,26) ***</td>
<td>27.25 (2,26) ***</td>
<td>7.33 (2,26) **</td>
<td>24.33 (2,26) ***</td>
</tr>
</tbody>
</table>

Notes: *P < 0.05, **P < 0.01, ***P < 0.001. Numbers in parenthesis represent numerator and denominator df.
Figure Legends

Figure 1. The means (± 1 SE) of density of new shoots of *Fargesia qinlingensis* in the three unflowered patches during the three-year period at the Taibaishan National Natural Reserve, Shaanxi Province, China.

Figure 2. The means (± 1 SE) of the density of live culms of *Fargesia qinlingensis* in the flowering sites and unflowered patches over three-year period at the Taibaishan National Natural Reserve, Shaanxi Province, China. Different letters indicate significant differences at $P < 0.05$ level.

Figure 3. The means (± 1 SE) of density of total seedlings of *Fargesia qinlingensis* in two sites (a) and two years (b), and means (± 1 SE) of density of seedlings established in 2004 in two sites (c) and two years (d) at the Taibaishan National Natural Reserve, Shaanxi Province, China. Different letters indicate significant differences at $P < 0.05$ level.

Figure 4. The means (± 1 SE) of seedling height (a), seedling leaf number (b), and seedling leaf length (c, d) of *Fargesia qinlingensis* at the Taibaishan National Natural Reserve, Shaanxi Province, China. Different letters indicate significant differences at $P < 0.05$ level.

Figure 5. The means (± 1 SE) of treatment combinations for seven chemical compound variables: (a) organic matter (OM), (b) crude protein (CP), (c) neutral detergent fiber (NDF) (lignin, cellulose, and hemi-cellulose), (d) acid detergent fiber (ADF) (lignin and cellulose), (e) hemi-cellulose (HC), and (f) ether extract (EE) (crude fat) in culms of *Fargesia qinlingensis* collected from the Taibaishan National Natural Reserve, Shaanxi Province, China. Different letters indicate significant differences at $P < 0.05$ level. Two samples of rhizome (flowering and unflowered) and one sample of seeds were also graphed for comparison but not included in analyses.

Figure 6. Mean (± 1 STD) height, branch number, leaf number, and seedling density for (A) control (C), nitrate addition (N), phosphorus addition (P), and combined N+P addition and (B) flowered and unflowered sites. Different letters indicate significant differences at $P < 0.05$ level.
Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.