FLOWERING AND FLOODING: FACTORS INFLUENCING SHOOT PRODUCTION IN A SEMELPAROUS BAMBOO

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FRANKLIN, D. C. & HOGARTH, N. J. 2008. Flowering and flooding: factors influencing shoot production in a semelparous bamboo. Culm recruitment by semelparous bamboos has been reported to be severely depressed in the year prior to flowering, providing forewarning of flowering and subsequent die-off. However, supporting data are scant. We monitored productivity in 30 clumps in a wild stand of the riparian bamboo *Bambusa arnhemica* for four years, following which the clumps flowered and died. Stand-level productivity in the year prior to flowering was a minimum of 78% lower than previous years. However, the rate of depression was unevenly distributed, being close to 100% among clumps lower on the river bank and no more than 50% higher on the bank. This may be due to the impact of early and prolonged flooding in that year. Clumps high on the bank may have benefited from favourable conditions associated with above-average wet season rainfall, raising the possibility that resource allocation to vegetative growth and sexual reproduction in semelparous bamboos is flexible.

Keywords: *Bambusa arnhemica*, clumps, gregarious monocarpy, northern Australia, recruitment, riparian vegetation

FRANKLIN, D. C. & HOGARTH, N. J. 2008. Pembungaan dan banjir: faktor yang mempengaruhi penghasilan pucuk dalam buluh semelpari. Penghasilan kulma oleh buluh semelpari dilaporkan menurun dengan banyak pada tahun sebelum pembungaan. Ini tanda amaran awal bagi pembungaan dan kematian. Namun, data sokongan adalah kurang. Kami memantau produktiviti 30 rumpun dalam dirian liar buluh riparian, *Bambusa arnhemica* selama empat tahun. Selepas ini, buluh berbunga dan kemudiannya mati. Produktiviti peringkat dirian pada tahun sebelum pembungaan yang minimum ialah 78%. Kadar penurunan tidak sekata—hampir-hampir 100% dalam rumpun pada kedudukan dekat tebing sungai dan kurang daripada 50% pada kedudukan lebih tinggi. Ini mungkin disebabkan kesan banjir awal dan berpanjangan pada tahun tersebut. Rumpun yang berada jauh dari tebing sungai mungkin mendapat manfaat daripada keadaan baik yang dikaitkan dengan hujan yang banyak semasa musim lembap. Ini mencadangkan bahawa pengagihan sumber bagi pertumbuhan vegetatif dan pembiakan seks dalam buluh semelpari mungkin fleksibel.

INTRODUCTION

Semelparous bamboos are widely reported to produce few or no culm shoots in the year prior to flowering (Troup 1921, Prasad 1987, Vazquez-Lopez *et al.* 2004). However, supporting data are scant (see Banik 1995 for an exception). The issue may explain the allocation of resources to vegetative and sexual reproduction, an issue of particular interest in clonal plants (e.g. Barsoum 2001, Brathen & Junttila 2006, Mandujano *et al.* 2007). It is also of practical relevance to bamboo culture because the loss of culm shoot production may be of immediate concern and may provide warning of impending flowering and death (Troup 1921).

In this study, we report recruitment rates over four years in a wild stand of *Bambusa arnhemica*, a gregariously semelparous bamboo from northern Australia (Franklin 2004), on the bank of the Adelaide River. The study was terminated when the stand flowered and died, so that we were able to compare recruitment rates in the year immediately prior to flowering with previous years. We then evaluated the possibility that recruitment rates in the year prior to flowering were also or alternatively influenced by the impact of flooding in that year. The rationale for considering flood effects arises from a demographic study of *B. arnhemica* on a

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lagoon bank on the Mary River 45 km away (D. C. Franklin *et al.,* personal observation), which commenced in the same year as this study. In the fourth year of that study (i.e. 2003/04, the wet season preceding flowering in this study), early and prolonged flooding was associated with severe depression of productivity in clumps low on the bank, but above average productivity of clumps at the highest level of the bank, with an 8.5 fold difference in productivity between those lowest and highest on the bank. This effect was not noted in other years in which flooding was later and less prolonged. Early and prolonged flooding was also observed on the Adelaide River in the 2003/04 wet season, associated with December rain that was over double the average and sustained by slight to moderately above-average falls in the following three months (Figure 1).

MATERIALS AND METHODS

Study species and area

Bambusa arnhemica is endemic to the monsoonal north-west of the Northern Territory in northern Australia, where it mostly occurs on floodprone river banks (Franklin 2004, Franklin & Bowman 2004). Culm recruitment takes place during the wet season (Franklin 2005). Notwithstanding considerable tolerance of inundation (Cowie *et al.* 2000, Franklin & Bowman 2003), its occurrence is constrained on the lower portion of major river banks by the frequency and/or length of inundation (Franklin & Bowman 2004).

The species is gregariously semelparous, flowering after an estimated lifespan of about 42 years (Franklin 2004). Flowering typically commences during the mid dry-season and continues until the early wet season (Bellairs *et al.* 2008).

The study was conducted on the bank of the Adelaide River at Owens Lagoon (12° 59' S, 131° 15' E). Soils were alluvial yellow-brown clay-loams. The climate of the area is intensely monsoonal with high temperatures throughout the year and intensely seasonal rainfall (Figure 1).

Field methods and data analysis

Survival and recruitment were monitored annually (2001 till 2004 inclusive) after the completion of recruitment for all culms (788 leafy culms initially and 350 subsequent recruits) on 30 clumps of mature vegetative-phase *B. arnhemica* on the bank of the Adelaide River. Each culm was tagged and its diameter (at

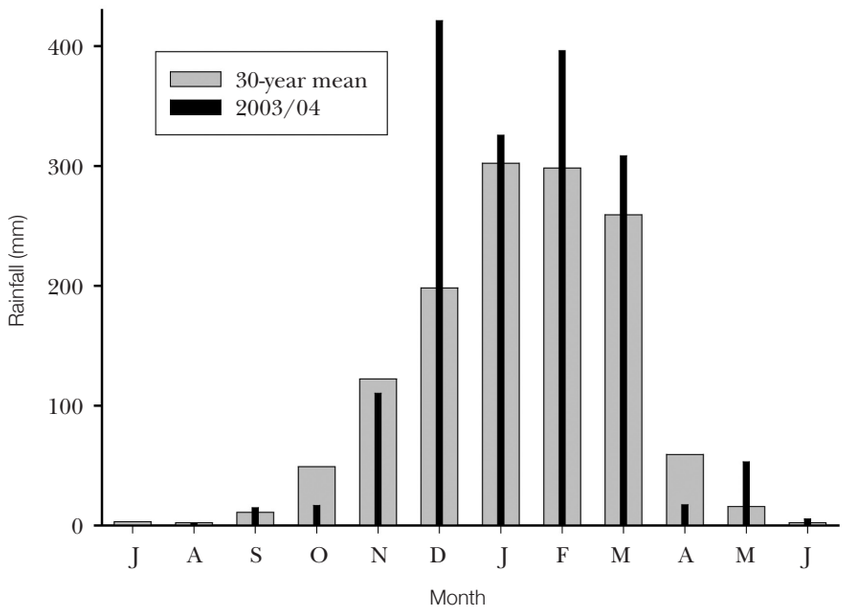

Figure 1 Monthly rainfall averaged over 30 years (1961–1990), and for the year prior to flowering (2003/04), interpolated for the degree cell containing the Owens Lagoon study site on the bank of the Adelaide River (Source: Bureau of Meteorology 2007)

the internode nearest 1.3 m) measured to the nearest 0.1 cm. Dead and senescent (leafless) culms were not considered. In the first year of the study, first-year culms were identified by the persistence of culm sheaths at least on the lower culm, by the fresh greenness of the culm surface and by the absence or nascent state of branching, stages of development that were verified over subsequent years as robust.

The vertical position of each clump on the bank was determined in metre classes using a metre rule and clinometer with the adjacent river as a benchmark.

In contrast to many bamboo plantations, wild *B. arnhemica* clumps are not evenly spaced, vary greatly in size and may contain more than one genet, and culms vary greatly in diameter (Franklin 2003, D. C. Franklin *et al.*, personal observation). For these reasons, our measure of productivity, which we subsequently refer to as the recruitment rate, is the basal area of recruits divided by the basal area of older culms leafy at the time of assessment, calculated for each clump. This measure has proven most informative in detailed demographic analyses (D. C. Franklin *et al.*, personal observation).

RESULTS

The basal area of recruits was depressed in 2003/04 by a minimum of 78.3% compared with previous years and the per clump recruitment rate by a minimum of 71.2% (Figure 2a). This was the result of a combination of reduction in the number of recruits (min. 49.2% reduction) and their diameter (min. 34.2% reduction) (Figure 2b).

The study clumps occupied a vertical range of 6 m on the river bank. In the year prior to flowering, recruitment rates varied significantly with position on the bank (Figure 3; Kruskal-Wallis $H_{6,29} = 13.86$, $p = 0.031$), being depressed to close to zero over the lower 5 m. Amongst clumps highest on the bank (7 m) the mean recruitment

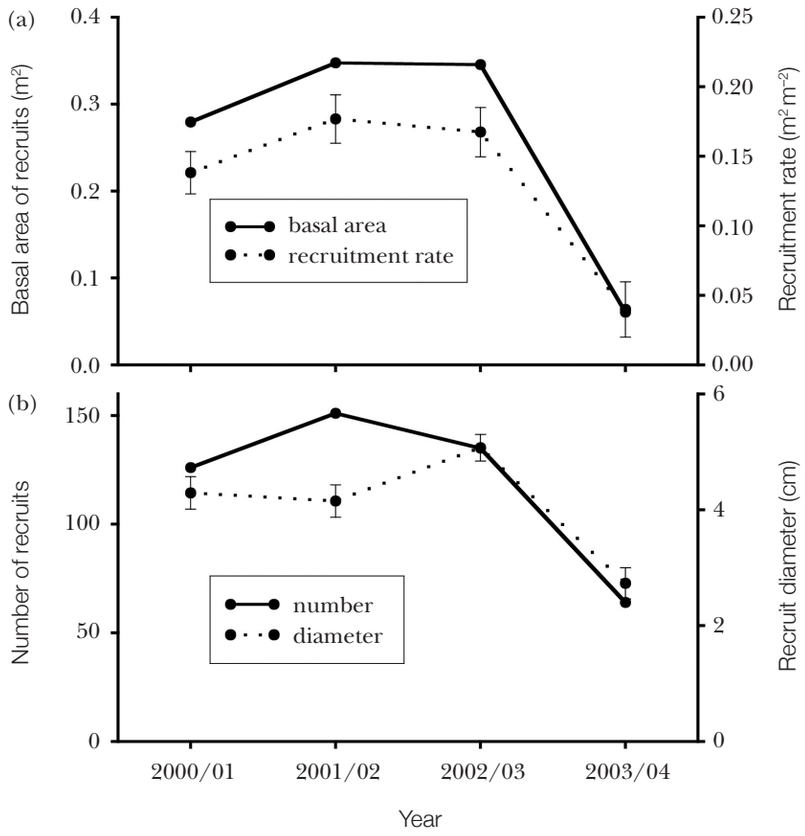

Figure 2 Annual patterns of culm recruitment by clumps of the tropical bamboo *Bambusa arnhemica* at Owens Lagoon: (a) total basal area and per clump rates (mean ± SE) and (b) total number and diameter (mean ± SE)

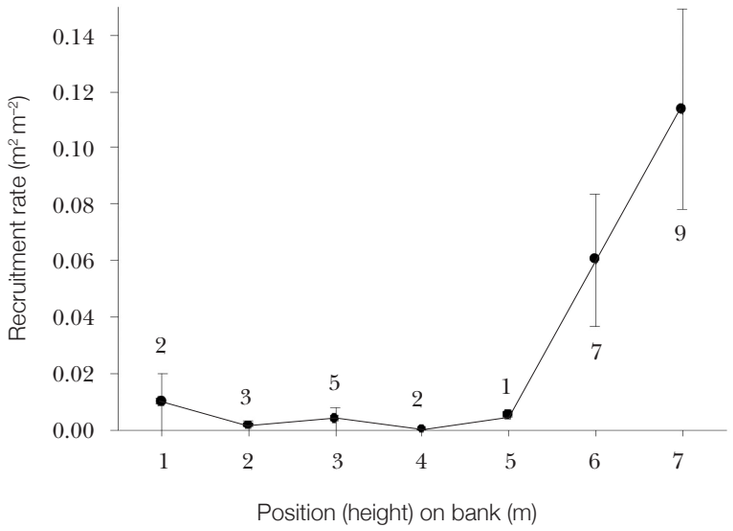

Figure 3 Culm recruitment (mean ± SE) by the tropical clumping bamboo *Bambusa arnhemica* in the year prior to flowering according to vertical position on the river bank. Numbers above/below estimates are the sample size (number of clumps).

rate was 0.113 m^2 m^{-2}, 18–36% lower than the means of 0.138 to 0.177 m^2 m^{-2} for all clumps in previous years (Figure 2a).

One small clump (three culms) died without flowering between the 2003 and 2004 assessments. When examined on 7 May 2005 with a view to assessing recruitment during the 2004/05 wet season, all remaining clumps were found to have flowered during the previous year and culms were mostly dead or dying. The exception was one clump (at level 3 m on the bank) for which we estimated that only 40% of culms had flowered, the other 60% of culms remaining leafy. When re-examined on 12 June 2007, all clumps were completely dead.

DISCUSSION

As reported for other semelparous bamboos, shoot productivity in *B. arnhemica* in the year prior to flowering was severely depressed—by about 75%. Banik (1995) reported 75–100% reductions in shoot production prior to flowering in four 'complete'-flowering Bangladeshi bamboos. However, we attribute a substantial portion of the decline in *B. arnhemica* to the impact of early and/or prolonged flooding. This study provides further confirmation of the important role of flooding in influencing the ramet dynamics of *B. arnhemica*, a role with real potential to account for the constrained distribution of *B. arnhemica* on stream banks (Franklin & Bowman 2003, 2004).

The cause of the 35–50% reduction in productivity of the clumps highest on the bank is uncertain. At a study site on the Mary River (at which *B. arnhemica* clumps did not subsequently flower), flood impacts on recruitment in 2003/04 were severe on the lower bank but recruitment was elevated at the upper levels (D. C. Franklin *et al.*, personal observation). We attributed the elevated recruitment among upper clumps to the positive effects of above-average moisture status that could be apportioned to either or both early wet season rainfall and/or brief periods of inundation. Moisture limitations during the early part of the growing season can influence the rate of production, timing and/or survival of culm shoots in a range of bamboo species (reviewed by Kleinhenz & Midmore 2001) including *B. arnhemica* (Franklin 2005).

This raises the speculative possibility of an interaction between flowering and rainfall in which flowering depressed productivity but this effect was partly mitigated by favourable conditions among the upper clumps. If this is the case, then resource allocation in bamboos in the year prior to flowering is flexible, favourable conditions perhaps providing an excess over requirements for impending flowering that may be allocated to further vegetative growth. Amongst non-semelparous clonal plants,

flexibility in commitments to alternate vegetative and sexual 'reproductive' strategies is common but sexual reproduction is often associated with favourable conditions and vegetative growth with less favourable circumstances (Chazdon 1991, Brathen & Junttila 2006).

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